THE DERMAL MORPHOLOGY OF MILLEROSTEUS MINOR

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INTRODUCTION

An historical analysis of the literature until the early decades of the present century

The first encounter with '*Coccosteus minor*' Hugh Miller (now *Millerosteus minor*) in the literature occurs in the year 1858, when Hugh Miller (1) was describing the fauna of a quarry to the south-east of Kirkwall, in the Orkneys (in what is now known to be Rousay Beds). While discussing his experience of often finding a single organism only in one locality of the Old Red Sandstone, Miller notes that in the quarry in question he 'found scarce a single fragment which did not belong to an exceedingly minute species of *Coccosteus*, of which my first specimens had been sent me a few years before by Mr Robert Dick, from the neighbourhood of Thurso'. These latter specimens had earlier been confused by Miller with the young of '*Coccosteus decipiens*' because of the similarities in general proportions yet discrepancy in size. This idea had been reinforced by its 'apparent gregariousness, too, quite as marked at Thurso as in this quarry', by analogy with extant fish which, while solitary as adults, are gregarious when young. He noted that 'this minute gregarious *Coccosteus*, so abundant in this locality that its fragments thickly specle the strata for hundreds of yards together – (in one instance I found the dorsal plates of four individuals crowded into a piece of flag barely six inches square)'. This phenomenon is now known for other fish of the Orcadian Old Red Sandstone and its explanation, which does not depend on the young being gregarious, will be more fully discussed in a later section. But by 1858 Miller had become of the opinion that this 'was not an immature, but really a miniature *Coccosteus*' on the basis that, although the tubercules of the larger

species increased in number with the growth of the individual, those of the minute form are as numerous as in '*C. decipiens*' (now *C. cuspidatus*, *Dickosteus* or *Watsonosteus*). Miller noted that the small coccosteids from Thurso and Kirkwall had a length, from snout to dorsal spine, of about one and a half to two inches, the entire fish being probably three or four inches ('not one-fourth of the size' of *C. cuspidatus*), and to this new species of *Coccosteus* he assigned the name *Coccosteus minor* (1, p. 395).

The confusion between this species and the young of '*C. decipiens*' remained, however, and to add to it mention was made, in a letter from Miller to Egerton, published in 1860 (2), of *Coccosteus pusillus* McCoy, another small form, which was figured in this publication. It is quite probable, though, that this *was* the young '*C. decipiens*'. This, indeed, was Traquair's impression: 'I rather think that *C. pusillus* McCoy is also a young specimen of the same species ('*C. decipiens*'), and if so, then the name *C. minor* Hugh Miller should be applied to the small Thurso specimens collected by Robert Dick, which most certainly are extremely distinct from the ordinary Moray Firth and Orkney examples of the genus' (3). The following year '*C. minor*' was figured by Traquair. Woodward gave a short description of '*C. minor*' in his 'Catalogue of fossil Fishes in the British Museum' (1891) (4) concentrating solely on the general shape of the larger plates, although noting the 'mandibular teeth very slender and sharply pointed' (see later).

Millerosteus began to assume importance as an index fossil and in 1908 Watson (5) described the first known occurrence of the species outside Thurso and Kirkwall, large numbers of plates being found in Hillhead Quarry, near Dalcross in Inverness shire. From this evidence Watson proposed that 'the Hillhead Quarry represents a different horizon to that of the ordinary nodules of Cromarty, Lethen Bar and Tynet Burn' (the latter now known to be equivalent to the Achanarras band in Caithness). These *Millerosteus*-bearing beds south of the Moray Firth are

undoubtedly equivalent to the Mey Beds in Caithness and Rousay Beds in the Orkneys, that is, the upper strata of the Thurso Flagstone Group. (One must be extremely careful of not introducing tautologous reasoning when distinguishing the beds solely on the grounds that they contain *Millerosteus*, evidence from both faunal complexes and lithology must also be sought when attempting to define the Mey Beds.) The implications of Watson's discovery will be discussed later.

Early accounts of the morphology of *Millerosteus* are rare, it being mentioned, usually only briefly, only in stratigraphical papers or, less commonly, in relation to other coccosteids; eg. Hussakof in 1911 (6) noted that in *C. canadensis* the 'lateral line (of the anterior dorsolateral) is noteworthy since it consists of two branches which diverge at an acute angle a short distance back of the articulating process. A similar branched canal occurs on the anterior dorsolateral in some other coccosteids, for instance *C. minor* and *C. magnus*'.

This introduction has amply demonstrated that, prior to the account by Heintz in 1938 (20), very little was known of 'C. *minor*', save that it was a very small fish, and not the young of '*C. decipiens*' as was '*C. pusillus*'. Subsequent to this paper by Heintz *Millerosteus* has only been alluded to on isolated occasions: Stensiö in 1963 (19) examined one specimen and attempted a restoration (of which a critique will be given later) based on the figures published by Heintz, while Miles did likewise in 1964 (23). Thus the present study is the first comprehensive one concerning itself with *Millerosteus*. It will concentrate mainly on the dermal morphology although the questions of affinity and the stratigraphical relationship to the other coccosteids of Lake Orcadie will also be considered.

THE STRATIGRAPHY OF LAKE ORCADIE AND ITS FAUNAL COMPLEXES

The classic study of the Middle or Orcadian Old Red Sandstone of Caithness, carried out by Crampton and Carruthers (7), showed a fairly simple succession of strata, the oldest of which appear at Sarclet, six miles south of Wick. These older rocks, comprising sandstones, mudstones and conglomerates, represent an area of upheaval which was centred on Sarclet. On either side of the axis, then, the strata became successively younger although, following the coastline, it is to the north-east, in the Ackergill Syncline, that the series of younger rocks continues to the greatest extent, as a nearly unbroken succession of flagstones occurring from the conglomerate base north of Sarclet to the John o'Groat's Sandstone. (These formations have their equivalents in the Orkneys.) To the south, in the Latheron Syncline, the series is not so complete, although many strata may be correlated with those of the Ackergill Syncline (eg, the Ousdale Mudstone is comparable to the Sarclet Mudstone, and the Berriedale Flags and Sandstone are equivalent to the Helman Head Beds of the Wick Flagstone Group).

The sequence of strata on the coast north of Sarclet as worked out by Crampton and Carruthers is shown in Table I. By way of confirmation, at least for the upper groups in the sequence, it was noted that Traquair (1894) had recognised three distinct faunae, those of the John o'Groat's Beds, the Achanarras quarry and the district from Halkirk to Thurso. It was only in the latter, he noted, that '*C. minor*' was to be found.

TABLE 1

John o’Groat’s Sandstone	
Thurso Flagstone Group	Mey Beds Thurso Flagstones Ackergill Beds
Position of Achanarras and Niandt Beds	
Passage Bed Group	Noss Beds Castle Sinclair Flags Field Beds Papigoe Beds
Wick Flagstone Group	Wick Beds Red Beds Helman Head Beds
Barren Group	Ellensgoe Conglomerate Ulbster Sandstone Mudstones Sarclet Sandstone Sarclet Conglomerate

It is in the Papigoe Beds (lithologically these are passage beds from the Wick type to the Thurso type) that '*Coccosteus decipiens'* first makes an appearance, and it was thought to continue through the other horizons of the Passage Beds, through the Achanarras band and into the Thurso Group. (Although, the authors of the Memoir noted, it was absent from the Ackergill Beds, *Millerosteus* being the only recorded coccosteid in these beds – for a discussion of this see later.) In fact, the Ackergill Beds were found to have faunal types, such as '*C. minor*' and *Glyptolopis paucidens*, which first made their appearance at this level, but which were also found in the rest of the Thurso Flagstone Group. But the relationship of the Ackergill Beds to the older Noss Beds was not clear for, along the coast, they occur on opposite sides of a fault (in actual fact three faults following one another closely, at Castle Girnigoe). At this time (1914) it was concluded that the reason for the sudden appearance of new genera was not, then, due to an abrupt environmental change but to the fault which 'at this point is a large one, and cuts out the basal members of the Thurso Flagstone Group with the horizon of the "Achanarras Band"'. Investigation of the Achanarras quarry inland (it is not represented on the coastal cliffs) by Crampton and Carruthers showed that *Glyptolepis paucidens* had already made an appearance by this time, although '*C. minor*' was absent. This quarry, just west of Spital, lies at the intersection of the Thurso and Wick Groups (the former north of a line from Spital, through Halkirk, to Reay, the latter to the south) and has its equivalent in the sandwick Fish Bed of the Orkneys. The Achanarras fauna (investigated by Traquair in 1894) also been found on the east coast of Caithness, in the flagstones of Niandt. Not only did Crampton et al. notice the presence of '*C. Minor*' in the black, bituminous shale of the Ackergill Beds (these fish bands being interspersed with sandstone) as well as in the equivalent fish bearing bands of the Mey Beds, but also these Beds were seen to

greatly resemble one another lithologically, being composed of pale blue or buff calcareous flagstones with fish remains, mudstones and bands of sandstone. They noticed at Thurso Bay and Murkle Bay yellow sandstone alternating with the *Millerosteus*-flagstones. It was concluded that *Millerosteus* was restricted solely to the Thurso Flagstone Group, where it was found to occur in all three divisions of their supposed sequence as well as in their Orkney equivalents.

The question naturally arises as to whether, besides *Millerosteus minor*, any other species are confined to the Thurso Flags. Geikie noted that, whereas *Dipterus macrolepidotus*, *Diplopterus borealis* and *Osteolepis macrolopidotus* had a wide vertical range that included both the Wick and Thurso Flags, *D. valenciennesii* and *O. arenatus* seem to be peculiar to the Wick Groups. In some of these findings he was incorrect for it in now known that *O. macrolepidotus* is confined to the Achanarras band whilst *D. valenciennesii* was found by Traquair (1894) throughout the entire range, from Wick to the Mey Beds. *Acanthodes*, *Diplacanthus* and *Parexus* (found in the Forfarshire flagstones) were only noticed by him in Caithness in the Thurso groups. But he observed correctly that '*Osteolepis microlepidotus'* (*O. panderi*) was characteristic of the Thurso group, but not below this level, and that the 'range of *Coccosteus pusillus* [Millerosteus]) is equally restricted'. Crampton at al. were able to add *Thursius pholidotus*, *Homosteus milleri* and *Glyptolepis paucidens* (as well as *Millerosteus minor* and *Osteolepis panderi*) to the list of fossil fishes that did not descend to the Passage Beds. As has been seen, many of the genera are found in the intermediate Achanarras quarry (Traquair, 1894, noted acanthodians, *Homosteus milleri* and *Glyptolepis paucidens*). What remains of the

fauna of the Thurso Flags is a mixture of genera that have their origins in the Wick, Passage and Achanarras Beds and continue into the Thurso Flags together with those species, such as *Thursius pholidotus*, *O. panderi* and *Millerosteus* which are first encountered in the Thurso Flags. (To this list of species peculiar to the Thurso Group has now been added *Homacanthus borealis* and *Gyroptychius milleri*.) Under the amended stratigraphical sequence of Miles and Westoll (see later) these species are seen to characterise not the whole of the Thurso Flags, but only the upper Mey Beds.

These conclusions received support from faunal studies on the Old Red Sandstone of the Orkneys (Watson, 1935) (9). The *Millerosteus*-bearing Thurso Flags of Caithness have their equivalent in the Rousay Beds of the Orkneys. Again '*O. microlepidotus'* is restricted to this zone, just as *O. macrolepidotus* is to that of the older Stromness Beds. Similarly '*C. minor*' and *Thursius pholidotus* are confined to this upper zone. Apart from these, the fauna of the Rousay and Stromness Beds were thought similar with many genera in common. The upper (Rousay) Beds are characterised by *Thursius pholidotus*, whilst the lower (Stromness) Beds are characterised by '*Pterichthys'* (it in now known that in Caithness '*Pterichthys*' (*Pterichthyodes*) in confined to the Achanarras band). *Dipterus platycephalus* is restricted to the Rousay Beds in the Orkneys, yet it may occur in the '*Pterichthys'* zone in Caithness.

The area covered by the conglomerates and breccias, flagstones and John o'Groat's Sandstone is enormous, far greater in size than the other basins of deposit of the Old Red Sandstone (of which Geikie* listed four – Lakes Caledonia, Cheviot, Lorne and the Welsh Lake). On the mainland of Scotland only its southern and western margin may be seen, these shores occurring in the Moray Firth region. (Watson's discovery (5) demonstrates conclusively that at the time of deposition of the Mey Beds Lake Orcadie's

[*who coined the name Lake Orcadie]

southern boundary must have been south of the Moray Firth and this allows a great extension of the geographical distribution of *Millerosteus* over the previously restricted Thurso-Kirkwall area.) The northern shores may be traced in the Shetlands, showing that the lake stretched over Caithness and the Orkneys. Its eastern boundary may be marked by the west coast of Norway, for around Sognefiord and Dalsfjord conglomerates similar to those in Scotland may be seen. Geikie further believes that 'the occurrence of a few species of fishes common to the Old Red Sandstone of the north of Scotland and of Russia goes far to show a connection, more or less restricted, no doubt, between these distant areas, or at least suffices to indicate that any watershed that separated them was not a wholly insuperable barrier to their respective faunas (8, p. 396). It must be remembered that during Middle Devonian times the first major continental deposits were being laid down (the 'Old Red Sandstone continent') and it is believed that the northern supercontinent at this time (Laurasia) extended from Leningrad to the Canadian plains, with its southern shore line (bordering the Tethys Ocean) running through southern Britain. On this count, then, Geikie could conceivably be correct. If he were correct, *Millerosteus* ought to be found in deposits in Europe as far east as Russia which are equivalent to the Spital and Mey Beds of Caithness (or at least a genus to which it shows an affinity). The extension of Lake Orcadie based on studies on the faunal complexes (of which *Millerosteus* was a member) will be discussed later. The Russian Old Red Sandstone deposits, however, show fish beds intercalated amongst rocks bearing marine fossils, indicating a sea-level delta deposit frequently subjected to marine invasions. The extensive marine transgressions of Middle Devonian times seems not to have been applicable to the Old Red Sandstone of Scotland, although this does not mean that it was discontinuous with the Russian deposits.

CONDITIONS AT THE TIME OF DEPOSITION OF LAKE ORCADIE AND THE ENVIRONMENT IN WHICH MILLEROSTEUS LIVED

The striking contrast of the Caithness flagstone series when compared to the Old Red Sandstone in other parts of Britain probably reflects deposition under dissimilar conditions. Both lithology and palaeontology point to a lacustrine origin for Lake Orcadie. The absence of beach deposits and the constant reoccurrence of mudstones with well defined sun-cracks in rapid alternation with calcareous flags through thousands of feet of strata bear out this contention. In fact, where marginal deposits are encountered (eg. at Red Point, near Reay) the even-bedded character of the flagstones is continued right up to the edge of the granite and gneiss. Near this junction chips of granite that were chipped off by subaerial flaking and fell into the mud now lie embedded in the flag exactly where they fell. There is no trace of a beach here, or of tidal scour.

The large number of fossil fish unique to the Orcadian deposits would lead one to assume some degree of faunal isolation and therefore non marine environment. Also the fossil plants (*Psilophytes*, the coniferous *Arancarioxylon* and *Caulopteris peachii*) obtained from the flags are definitely of continental origin, as is the giant eurypterid *Pterygotus*. But the most important evidence is offered by the presence of the crustacean '*Estheria membranacea'*. The extant *Estheria* occurs on all six continents in stagnant pools, marshes and occasionally brackish water but never in marine conditions. This genus in the past has always been associated with fresh water creatures and is undoubtedly indicative of land-locked waters. Watson (9) believed that the great numbers of dipnoans and crossopterygeans found in the flags (including the osteolepid *Tristichopterus* in the John o'Groat's Sandstones which he thought ancestral to Eusthenopteron of the Upper Old Red Sandstone of Scaumenac

Bay Canada), ie bony fish which ‘possessed an air bladder which was a functional lung and enabled them to breathe air when necessary and thus to live in shallow water which had become deoxygenated by the decay of organic detritus’, was indicative of a fresh water habitat.

In attempting to explain the origin of the tetrapods Lull (1918), and following him Romer, postulated seasonal variation in climatic conditions from wet to semiarid as the cause of the transition. According to this the pools would dry up completely during these periodic dessications and the stranded rhipidistians would be forced to move to another pool to continue life as fish. (This idea has been modified somewhat, without altering it in essence, by Eaton (1960) postulating, not the complete drying up, but only partially so. Those fishes having lungs were then forced out due to competition etc.) The ichthyostegids, the earliest amphibians in which the fin is known and for which the theory is supposed to apply, are to be found in the very late Upper Old Red Sandstone of Greenland. At this time Greenland was in close proximity to the Orcadian region and the environmental conditions conjectured for one must also apply to the other (the appearance of the North Atlantic ridge was subsequently to drift westwards).* Yet the ichthyostegids are well-developed Amphibia, so the preceding transition must have been long – probably extending back into the Middle Devonian – and these climatic conditions must also have been prevalent at this time. In fact this is borne out by many other factors, not the least being the great numbers of lung-bearing fish. The mudstones in Caithness reveal sun-cracks indicating drying out and exposure and also pitting from rain, presumably heavy rains in the alternate season.

[*It is interesting to note in Wilson et al. (p. 140) reports of ‘tracks’ in the Red Glen (Hoy Sandstone) of the Upper ORS although these have not been seen since.]

This theory would not, unfortunately explain the abundance of coccosteids for, seen in relation to the bony fish, they would have been at a distinct disadvantage in the type of environment which necessitated the uptake of atmospheric oxygen. Even under the conditions conjectured by Eaton (1960), in which the pools only diminished in size and caused overcrowding, those fish survived that were able to prop themselves up on the substrate to gulp air. Could it be that the coccosteids possessed lungs too? There is no direct evidence for the Arthrodira, however Denison (1941) suggested that *Bothriolopis*, of the order Antiarchi, possessed them, although this view has been contested.

Perhaps, as is earlier suggested by Watson in his paper (9), the reason for the abundance of dipnoans is that they are the first animals in the food chain (being the 'only known fish in the fauna which could by any possibility be plant eating'). The only invertebrate known is '*Estheria membranacea*' (*Asmussia murchisoniana*) and this has a limited distribution, although it probably formed the food supply of the toothless acanthodians which were fed upon, in turn, by the predaceous osteolepids. The bitumunous nature of the flags was thought, by Watson, to indicate a region of lush plant growth. Similarly Geikie reports large sheets of matted *Psilophyton* becoming entombed in the mud of Lake Orcadie. It is possible that the acanthodians and dipnoans were at the base of their respective food chains, the predators being the osteolepids and coccosteids.

The habitat of *Millerosteus* may be summarised as follows. The lake at the time of deposition of the Mey Beds was extensive, *Millerosteus* being known to occur as far apart as the Orkneys and Dalcross, so its range was probably over the entire area of the lake. (Occurrences of *Millerosteus* outside of Caithness will be discussed later.) That the lake was shallow is shown by the mixture of terrigenous silts, organic debris and calcareous precipitates, together with ripple marks on the surface and evidence of pitted rain marked areas. This shallowness meant that there

were many flood plains subjected to seasonal drying up and giving rise to the sun-cracked mudstone, leaving only channels which traversed the mudflats (7, p. 94, 103), as shown by the fragmented fish remains, finely divided plant debris and greater degree of sorting of the deposits. This alone would suggest the seasonal isolation of small lagoons which, even if they did not completely dry out as Eaton suggests, would cause the asphyxiation of the fish and their entombing in the mud. Indeed, concentrations of fish are known in many instances from the record. Geikie (p. 401) has noted that in the lower strata of the Thurso group, '*O. microlepidotus'* is 'remarkably abundant. As many as a hundred individuals may be counted within a space of three or four square feet, mingled with remains of *Acanthodes* and *Cheiracanthus*'. The author has similarly examined a specimen of rock from the Wick formation containing possibly a dozen skulls of *Thursius*. This theory of isolation and asphyxiation would also explain the occurrence of many specimens of *Millerosteus* noticed by Miller in the 'Cruise of the Betsey' and by many other authors subsequently. Although there is a reasonable degree of probability that these represent examples of stranding and asphyxiation of contemporaneous individuals, yet catastrophic events of this sort should strike a cross section of the fauna. The enigmatic situation of only finding an abundance of one species in one locality can only be explained by assuming that our samples represent the respective niches of the different species, although how to account for the lack of the close association of species on which, eg. the osteolepids, preyed is problematical.

The rising water level in the lake was matched by the concomitant increase in the depth of the deposits, so retaining its shallowness. The water supply was undoubtedly river systems that fed the lake. When the Achanarras and Niandt bands are encountered there is a sudden increase in the fauna. It being clear that this fish fauna could not have evolved from that known in the underlying beds we must look for an origin elsewhere. It is known that the delta and flood plains were expanding at this time as the lake increased in area, so it is probably the case that barriers to faunal movement were being broken down with the advancing of the shore line (eg. by the joining of river systems or deltas), causing the lake to become joined to other regions of deposit in the area. An analogy presents itself in the form of lake Chad which ‘is believed to form but one of a chain of lakes which formerly connected the river basins of the Nile and Niger, since its fish fauna shows strong affinities with those of both river basins. while also having a few peculiar species of its own’ (7, p.103). This being the case, might the principle not be applied to the unique fauna of the Thurso Flags (*Millerosteus*, *Thursius pholidotus*, *O. panderi*, *Homacanthus borealis* and *Gyroptychius milleri*)? Perhaps faunal infiltration from an adjacent area was facilitated by the joining of the great wandering water courses feeding or draining the lake with those of neighbouring areas. Coastal erosion would certainly be able to cause the change of direction of these water channels. It is also possible that the shores of Lake Orcadie encroached upon those of lakes on the Continent, in which case it should be possible to find coccosteids in these areas, which may give a clue to the derivation or affinities of *Millerosteus* (see later).

RECENT STUDIES ON THE FAUNAL RELATIONS OF MILLEROSTEUS AND THEIR BEARING ON STRATIGRAPHY

Within the last decade the studies of Miles and Westoll have thrown new light on both the faunal complexes and stratigraphical relations of the Orcadian Old Red Sandstone. These authors (10) have shown that all known occurrences of '*Coccosteus decipiens'* in beds above the Achanarras band are, in fact, attributable to new genera and species, and, furthermore that '*C. decipiens'* is only a synonym for *C. cuspidatus*. Above the Achanarras band *C. cuspidatus* is completely replaced by *Dickosteus threiplandi* (ie. in the Spital, Mey and Rousay Beds). These authors were also able to show that what was thought to be '*C. decipiens*' found in the Eday Beds of the Orkneys is also a new genus and species, which they have named *Watsonosteus fletti*. This being the case, the position has now arisen where, not merely is *Millerosteus* confined to one horizon, but so are *Coccosteus cuspidatus*, *Dickosteus threiplandi* and *Watsonosteus fletti*, according to the following table:

*Coccosteus cuspidatus**	Achanarras				[Older
Dickosteus threiplandi		Spital	Mey		↓
Millerosteus minor			Mey		↓
Watsonosteus fletti				Eday	Younger]

This simplifies the problem somewhat and is more in accord with the author's theory of the derivation of the new genera. Rather than having to explain the appearance of one new genus (*Millerosteus*) in association with one ('*C. decipiens*') whose history is not confined to that horizon, the Mey and Spital Beds now see the appearance of two new genera. There is now a complete successional replacement of one coccosteid fauna by another upon changing horizon. The theory previously put forward by the author to account for the appearance of *Millerosteus* finds an even better example in the total disappearance of one coccosteid fauna and reappearance of another.

[*Saxon has found overlap of *Coccosteus* and *Dickosteus* in Spital]

Here the conditions in this region of the lake had altered concomitantly with, or inextricably linked to, the rising of the waters and floor of the lake and thus spread of the lake in area, giving rise to greater contact with surrounding niches. These new genera, having migrated from other localities, showed greater adaptation to the environment and so replaced the endemic *C. cuspidatus*, which then died out. This theory receives support from Miles and Westoll (10), the authors claiming that 'The apparently complete replacement of *C. cuspidatus* in strata immediately overlying the Achanarras band may rule out the evolution of the *Dickosteus* "population" of, say, Spital from the earlier *Coccosteus* "population" of Achanarras. A more plausible explanation is that *Dickosteus*, having developed in some nearby region, became able, probably due to subtle changes in the environment, to extend its range into Coccosteus territory and eventually to take over the position previously occupied by Coccosteus in the community' (p. 194). Furthermore, although *Dickosteus* occupies a large part of the Thurso Flagstone group and possibly overlaps the range of *Millerosteus minor*, 'it is not generally found associated with that form and is, on the whole, specially characteristic of strata below those bearing *M. minor* in the Thurso Flagstone Group' (p. 195). Undoubtedly, *Millerosteus* also migrated into the locality and competition brought about the replacement of *Dickosteus* by it, as is testified by the younger strata. The embarrassment of attempting to explain how changing conditions and the introduction and obvious adaptation of a new species could leave the indigenous population unaltered has been removed. A whole new fauna was introduced, only those species that were readily adaptable being able to remain within the changing niche. A more viable faunal complex had invaded the area when the watershed isolating them had been removed.

Miles and Westoll were only able to acknowledge the presence of *Coccosteus cuspidatus* in the Papigoe and Field Beds (the early Passage Beds of Crampton et al.) and in the Achanarras band, but in no higher levels. *Dickosteus threiplandi* was only found to occur in the Thurso Flagstone Group and in the Noss Beds (the highest Passage Bed of Crampton et al.) but not in the supposed intervening Achanarras bands. That the Papigoe and Field Beds are related is not only shown by the presence in both of *C. cuspidatus*, but also by the 'Papigoe-type' limestone beds containing these fossils. The Castle Sinclair and Noss Beds present a dissimilar lithology and, partly because the latter is known to contain *Dickosteus*, these beds are referred by the authors to the Thurso Flagstone Group. This view is reinforced by the resemblances of the Noss Beds to those at Scrabster, which had been noted by the Survey officers. Consonant with this is the conviction held by Miles and Westoll that the Noss and Castle Sinclair Beds should be placed above the Achanarras bands. This they justify by recourse to the stratigraphical intervals between successive strata. They estimated that between Achastleshore (where 'Papigoe-type' limestones are first encountered) and the Robbery Head Limestone the sequence is equivalent to 1600 ft in thickness, yet this only represents the 'Papigoe' and 'possibly also the lower part of the Field Beds'. The Survey, however, estimated the Field Beds to be 700 ft. in thickness and the Achanarras (Niandt) bands to be only 2200 ft. above the earliest 'Papigoe' Beds. (They, themselves, estimated the Papigoe and Field Beds to be only 1700 ft. in thickness but thought that some beds had been cut out by faulting.) These results would be more in accord if the later Passage Beds were transferred to a position above the Achanarras band. This leaves the sequence of Papigoe, Field and Achanarras Beds, all of which were shown to contain *C. cuspidatus* by Miles and Westoll.

Miles and Westoll have also reclassified the various strata of the Thurso Flagstone Group, and in so doing have demonstrated the errors in the supposed sequence elucidated by the Survey officers. Firstly, they showed a strikingly similar fauna in the Ackergill and Mey Beds (*Millerosteus*, *Thursius pholidotus*, *Glyptolopis paucidens* and '*Estheria*' – which should, they point out, be referred to *Asmussia murchisoniana*), as well as similar lithology. These beds, which they considered to be part of the same sequence, lie immediately below the John o'Groat's Sandstone and may be considered the equivalent of the Rousay Beds of the Orkneys, the latter lying immediately below the Eday Beds. If, as had been previously thought (eg. by the Survey), the Ackergill Beds were the lowest of the Thurso Flagstone Group, then they ought to be equivalent to the Upper Stromness Flags of the Orkneys for, according to the Survey, the Thurso Flagstones are equivalent to the Upper Stromness Beds and the Rousay Beds. Yet Westoll (11) had already noticed in 1951 the absence of the Ackergill fauna in the Upper Stromness Flags (there being only '*C. decipiens*', which is most probably *Dickosteus*, although this is, as yet, unverified).

Crampton et al. noticed that the 'Thurso Flags' (the middle of the three strata in the sequence) at Skirsa actually underlie the John o'Groat's Sandstone, yet postulate unconformity to explain this. Miles and Westoll show this to be an unnecessary assumption, it being more probable that these 'Thurso Flags' are also equivalent to the upper part of the Mey Beds on the north coast. In fact, in some areas of the 'Thurso Flags' (Duncansby Head, Skirsa Head on the east coast) there are bands of red and yellow sandstone (as there are in the Mey Beds of the north coast) which resemble, upon closer examination, the sandstone of the John o'Groat's types. This would be expected if the two strata were adjacent in the sequence. Although many other characteristic Mey Bed fossils are to be found in these

younger ‘Thurso Flags’ on the east coast, *Millerosteus* has so far not been recorded in either the Skirsa or Nybster area. It is conceivable that the ‘Thurso Flags’ in these areas represent the youngest part of the Mey Beds immediately prior to the Upper Middle Old Red Sandstone, by which time *Millerosteus* had vanished or been replaced, although the conditions at the time (as far as can be foretold from the record) had not given way to those causing John o’Groat’s Sandstone formation. A considerable facies change at the time of deposition of the youngest Mey Beds is not really acceptable, for *Millerosteus* is recorded from this horizon on the north coast (ie. those Mey Beds on the north coast containing bands of red and yellow sandstone). It is unlikely that conditions on the east coast were already approaching the John o’Groat’s Sandstone type, while those of similar lithology on the north coast were not. Although the Mey and Huna areas on the north coast (ie. those containing the red and yellow bands) contain *Millerosteus* (eg. East of Murkle Bay, Pennyland), it is unrecorded from the less sandy area between Thurso River and Murkle Bay, the reason for which is unknown. That these are Mey Beds is demonstrated by similar lithology and the fact that all other Mey Bed faunal members are present. It would seem, then, that apart from the last regions of deposit of the Mey Beds on the east coast, where *Millerosteus* is absent (as are some other members of the faunal complex in certain of these localities, eg. *Homosteus* and *Asmussia* from Skirsa), the characteristic fauna of the Mey Beds comprises *Millerosteus minor*, *Thursius pholidotus*, *O. panderi*, *Glyptolopis paucidens*, *Homosteus* and *Dipterus*.

The high position in the Thurso Flagstone Group of the ‘Ackergill Beds’ (ie. at some distance from the Achanarras band) may be demonstrated, for *Asmussia* and bituminous shales of the Mey-Ackergill type are to be found at Upper Killimster, some 2000-3000 feet lower than the ‘Ackergill’ outcrop on the east coast. From this it can

only be deduced that those exposures on the coast formerly considered to represent the lower sequence in the Thurso Flagstone strata must, in fact, lie at least 2000-3000 feet above the base. As the thickness of the Thurso Flagstone Group was estimated by the Survey to be 5000 feet, and as the 'Ackergill Beds' are thought to be those immediately underlying the John o'Groat's Sandstone, it is highly probable that Upper Killimster deposits are themselves some distance from the Achanarras band.

Furthermore Miles and Westoll were able to show that between the beds with the representative fauna just enumerated (Mey Bed fauna) and the Achanarras band with its fauna lay another stratum, also with a characteristic fauna. This fauna was found lacking *Millerosteus minor*, *Thursius pholidotus*, *Glyptolopis paucidens* and the crustacean *Asmussia* (there being an exception to the latter). However *Dickosteus threiplandi* is abundant, it being found in the quarries of Spital and Banniskirk, which are thought to lie 400-500 feet above the Achanarras band. This stratum may be followed, there being a consistent eastward dip, until Loch Scarmclate, which is thought to be 1000 feet above the Achanarras band. This 1000 feet of rock from Loch Scarmclate to the Achanarras band, then, holds a faunal complex preceding that of which *Millerosteus* is a component. The appearance of certain species characteristic of the Mey Beds occurs just above this 1000 foot horizon, for the Weydale, Youkil and Stonegun quarries are situated just above this level, and it is in the latter that *Thursius pholidotus* appears, whilst it is in the first and last named that *Osteolepis panderi* ('*O. macrolepidotus*') makes an appearance.* *Millerosteus*, however, is not found, yet these quarries are regarded as being the earliest of the Mey Beds.

[**Asmussia* has been found by Saxon at Stonegun quarry.]

It would appear then that Miles and Westoll (10, pages 199, 202-203 c and f) believe that the Spital Beds (containing the 'Noss Head Beds', there being faunal (ie. *Dickosteus*) and lithological resemblances) are characterised by the absence of *Millerosteus*, *Th. pholidotus*, *O. panderi* and *Asmussia*, and conversely that the appearance of these marks the opening of the Mey Beds. Yet Saxon (12) believes that Brims Ness and Holborn Head are Spital, although Miles and Westoll estimated the distance of these above the Achanarras band to be 5000 and 2600 feet respectively (assuming no faulting). If Saxon were correct then unconformity must explain the anomaly, for the Spital Beds have been shown to be 1000 feet elsewhere, as are the Upper Stromness Beds. Saxon believes furthermore that Stonegun is not Mey but Spital. Holborn Head, Brims Ness and Stonegun all contain *Th. pholidotus* and *O. panderi*, from which it would appear, if Saxon were correct, that *Millerosteus* is the sole index fossil for the Mey Beds. What does become apparent, though, is that *Millerosteus* is to be found in the fossil record later than *Asmussia*, *Th. pholidotus* and *O. panderi* (the dispute concerning itself with whether the latter occur in only the Mey Beds or both).

Until such time as more evidence becomes available to construct the Spital-Mey chronofaunal complex, it can only be concluded that *Millerosteus* occurs in the late Mey Beds (and even at this time not in all regions, eg the east coast) but not in the earlier Mey Beds, in a faunal complex that comprises:

Dickosteus threiplandi, *Millerosteus minor*, *Homosteus milleri*
Diplacanthus striatus, *D. longispinus*, *Cheiracanthus* sp.
Mesacanthus peachi
Thursius pholidotus, *Osteolepis panderi*, *Gyroptychius milleri*,
Glyptolepis paucidens
Dipterus valenciennesi (few)   *Asmussia*

Yet the time of origin (whether Mey or Spital) of many of these other faunal members must remain, for the present, obscure, awaiting an adequate definition of the boundary of the Mey and Spital Beds.

As a consequence of Miles and Westoll's study the correlation of strata between Caithness and the Orkneys has become simplified. It will be remembered how Watson (1935) had distinguished the *Millerosteus* and *Th. Pholidotus*-bearing Rousay Beds from the older beds which were characterised by '*Pterichthys'* (ie. the Achanarras band). In the Orkneys memoir Wilson et al. (13) thought the Thurso Flagstones equivalent to the Rousay and Upper Stromness Flags, their comparison between the regions being as follows:

ORKNEYS	**CAITHNESS**
Eday Beds..	John o'Groat's Sandstone
Rousay Beds \	Thurso Flagstone Group
Upper Stromness Flags /	
Sandwick Fish Bed...................................	Achanarras band
Lower Stromness Flags............................	Wick Group

The authors further note the occurrence of '*C. decipiens*' in the Lower Stromness Flags, Sandwick Fish Beds and Upper Stromness Flags, and it was also believed that this species was found in the Rousay Beds. Miles and Westoll (10) were able to verify the presence of *C. cuspidatus* in the Lower Stromness Flags, and the presence of this species in this and the succeeding bed would indicate the equivalence of these beds with the Passage Beds (Papigoe and Field Beds) and the Achanarras band of Caithness. Furthermore Miles and Westoll were unable to find any *C. cuspidatus* above this horizon; they did, however, find *Dickosteus threiplandi* in the Upper Stromness Flags, which would indicate that this bed was equivalent to the Spital Bed of Caithness.

Watson, in 1927, (54) had commented on 'two specimen of interest from the Rousay Beds (sic) of the parish of Kirkwall', one of which came from near Inganess Farm and was 'part of the exoskeleton of a large Coccostean' which 'differs from *C. decipiens* most markedly by the absence of a spine at the posterior end of the dorsomedian plate'. He noted that the B.M.(N.H.) had a similar specimen (from Traquair's collection and thought by him to be '*C. decipiens*')

which Flett (15) believed from the Eday sandstone of Newark Bay, Deerness. At this time Watson thought it ‘possible that it is restricted to a definite horizon’ for it had not been found in association with *Tristichopterus* (which was characteristic of the Eday Beds). Watson in 1931 described these two specimens and a third from Newark (16), raising it to a new species *Coccosteus fletti*. Again, in this publication he is of the opinion that the specimen occurring at Inganess Farm, together with the Newark specimens, may prove the limited horizon in which this species occurs is at the base, or below the base, of the Eday Beds ‘and it may ultimately serve to mark off a definite horizon towards the summit of the Rousay Beds’.

In their investigation of *Watsonosteus fletti*, Miles and Westoll concluded that Inganess Farm, thought by Watson and the Survey to be Rousay Beds, are, in fact, ‘passage beds’ and more properly placed in the Lower Eday Sandstone. The transition was noted to be ‘in places ... quite gradual through considerable thicknesses of strata’, so, on account of the occurrence of *Watsonosteus*, the line marking off the lowest horizon of the Eday Beds should pass below Inganess Farm. This position must now be adopted because all other localities bearing *Watsonosteus* are Eday Beds and the vertical range of *Watsonosteus* in the Eday Beds is not, as Watson had believed, limited but quite extensive. Also the members of the characteristic Eday fauna (first shown by Traquair in 1897 and 1898 to consist of *Tristichopterus alatus*, *Microbrachius dicki* and *Pentlandia macroptera*), unnoticed by Watson in the same horizon as *Watsonosteus*, have subsequently been found by Westoll (10, page 206) associated with *Watsonosteus* at Inganess Farm, hence this horizon must be considered at the base of the Eday Beds rather than below it.

It seems that, at least in the Orkneys (for the John o'Groat's Sandstone is not known to contain *Watsonosteus fletti*)* the characteristic placoderm of the Upper Thurso group (Mey Beds), ie. *Millerosteus minor*, was replaced by *Watsonosteus fletti* when conditions leading to the deposition of the Eday Beds were first encountered. This completes the temporal sequence, according to which at several times during the Middle Old Red Sandstone period a new genus of coccosteid assumed dominance in Lake Orcadie, this being linked either to climatic changes, or the breakdown of watersheds and increasing competition or, more probably, a combination of these two factors acting in conjunction. The sequence runs *Coccosteus cuspidatus* (passage Beds and Achanarras band), *Dickosteus threiplandi* (Spital and lower Mey Bed), *Millerosteus minor* (upper Mey Bed, although possibly disappearing before the sequence alters) and *Watsonosteus fletti* (Eday Beds)**. But as more information becomes available it appears that these are not absolutely distinct temporally (indeed, one would not really expect this) but some overlapping occurs. Miles and Westoll believe that *Dickosteus* overlaps *Millerosteus*, although the two are separated spacially, and Saxon now believes that *Coccosteus* occurred in the Spital Beds where it overlapped *Dickosteus*. It must be noted, however, that this is not a sequence in isolation for *Homosteus milleri* is known throughout a large part of the sequences from the Achanarras band to the Mey Beds. Although it is not strictly valid to imply that this series reflects replacement of one genus by another, for they may not have been in competition with one another or even have occupied similar niches, yet it seems reasonable to infer that some sort of successional replacement was in order, through the introduction of forms showing increased adaptation to the changing environmental conditions.

As already noted, lack of transitional forms in the fossil record implies a series of migrations from other localities, either due to the breakdown of physical barriers, or to changing environmental conditions encouraging the spread from other areas and the ensuing extinction of the indigenous faunas.

[*it is now known in John o'Groat's sandstone]

[**and perhaps (the antiarch) *Asterolepis orcadensis* locally (Watson [9])]

It will now be necessary to search for those areas adjacent to, or part of, Lake Orcadie, which could provide the source of these migrations, with special reference to *Millerosteus minor*. As a corollary the former extension of Lake Orcadie may be estimated.

OCCURRENCE OF MILLEROSTEUS MINOR OUTSIDE SCOTLAND

Gross (17) reports that a very small nuchal plate, measuring 12 mm long and 15 mm wide, had been found near the Gorodenko river in the Baltic, but his published photograph is far too small for positive identification to be made. He himself found a very small, finely tuberculated median dorsal plate, measuring 13 mm long and 9 mm wide, with a low inner keel and smooth inner surface in the same strata (which he refers to DM2). These coccosteids were not thought by him to be the young of '*C. livonicus*', the dominant coccosteid of the lowest strata of the Baltic Middle Old Red, (now referred to *Plourdosteus*) but rather '*C. decipiens*' or '*C. minor*'.

In fact the length of the nuchal of '*C. livonicus'* is given by Gross as 6 cms, while that of a large *C. cuspidatus* adult is only 3.3 cms long. As the youngest *C. cuspidatus* is always smaller than the largest *Millerosteus minor* (18) then it is extremely improbable that these small coccosteids reported by Gross could be the young of '*C. decipiens'* let alone '*C. livonicus*'.

Indeed, these measurements compare fairly well with those made by the author of equivalent plates of *Millerosteus minor*, as the following table shows:

No.	**Nuchal (length x width, mm)**	**Median Dorsal (length x width, mm)**
C. 369	10 x 14	32 x 15
C. 353		Length 29
C. 358		Length 24+
C. 376		20 x 9
C. 368		21 x 11
C. 362	8 x 11	
Gross's Specimens	12 x 15	13 x 9

The nuchal compares well, it being only 1 mm broader and 2 mm longer than that of C. 369; furthermore the length/width ratio of the Scottish specimens average 0.72, whilst Gross's specimen is 0.8 (cf. the nuchal of '*C. livonicus*' with a ratio of 1.0). Greater difficulty is encountered with the median dorsal plate, for although the width of the smallest UCL specimen (C. 376) is also 9 mm, in the latter the length is 20 mm whilst in Gross's specimen it is only 13 mm. Whereas in the Scottish specimens there is a width/length ratio of just under 0.5, in Gross's specimen it is near 0.7. The short length of the median dorsal could be accounted for by supposing the long dorsal spine to have broken off (as it has in many of the UCL specimens, although it would be difficult to account for 7 mm in this way; perhaps the anterior end of the median dorsal had also broken as it has in C. 358). Alternatively this may be a species without the long dorsal spine (Gross makes no mention of it) and with a short median dorsal (on this hypothesis *Millerosteus* should not be considered a monotypic genus).

These finds occurred in the DM2 beds of the Baltic States. Gross believes the beds DM1-3 correspond with the Achanarras and Thurso Flagstone Groups of Scotland and this conclusion has been accepted by Westoll (11). Westoll also notes that similar floras occur in Thurso, Stromness and Rousay Beds as in the Pernau sandstones of the Baltic (DM1-2). Furthermore Gross notes that Obrutschew (1932) had found a new species of *Coccosteus* in the equivalent beds of north west Russia, which he presumed to be '*C. cf. minor*'. These finds indicate that it is possible that the range of *Millerosteus* covered an area from Caithness and the Orkneys, where it is common, to the Baltic and even north western Russia. The repeated marine transgressions in these latter areas would ensure that the freshwater fauna had continually migrated there from more westerly regions where such transgressions are not known to occur.

DERMAL MORPHOLOGY OF MILLEROSTEUS MINOR

The collection of the specimens and their preparation

The present study is entirely based on specimens belonging to the Zoology Dept., University College London, and the British Museum (Natural History). The former have the prefix C in their number, the latter P. C. 369 and the other articulated specimens (C. 349, C. 353 and C. 375), on which the descriptive morphology is mainly based, were all collected from Pennyland, Thurso, in 16.4.66, although other specimens came from Murkle Bay. Some of the specimens required only little mechanical or acid treatment, although all required some. C. 369, which had about 60% of its surface covered by matrix (plate 1) necessitated extensive preparation; about 80 hours being spent in the mechanical preparation of this one specimen alone (for result see plate 2). The matrix is calcareous and thus amenable to treatment with dilute formic acid. The procedure was to immerse the specimen in acid for a period from 10 minutes to 1 hour (depending on the susceptibility of the flag to attack by acid, as judged by the reaction speed) and then to dry overnight in an oven. The surface matrix was then removed mechanically by means of a mounted needle (an electric needle was used on only one occasion, to clear the matrix from the border of C. 369) before re-immersion in the acid. Some specimens were more susceptible to attack by acid than others and the strength of the acid was varied accordingly, although the optimum concentration was usually about 10%.

The completely articulated C. 369 has dermal bone that is black in colour and well preserved (due to its being covered by matrix, preventing erosion) and is set in a pale brown matrix, although the matrix approaches grey in other specimens. C. 349 is also well preserved but the other two specimens show some wear due to erosion with consequent loss of much of the ornament; the dermal bones have become paler in colour and have an opaque bluish tinge. Crushing is not severe in any of the specimens, although it has occurred to a greater extent in C. 353 and C. 375 than in C. 369 and C. 349.

Plate 1

C. 369 before preparation

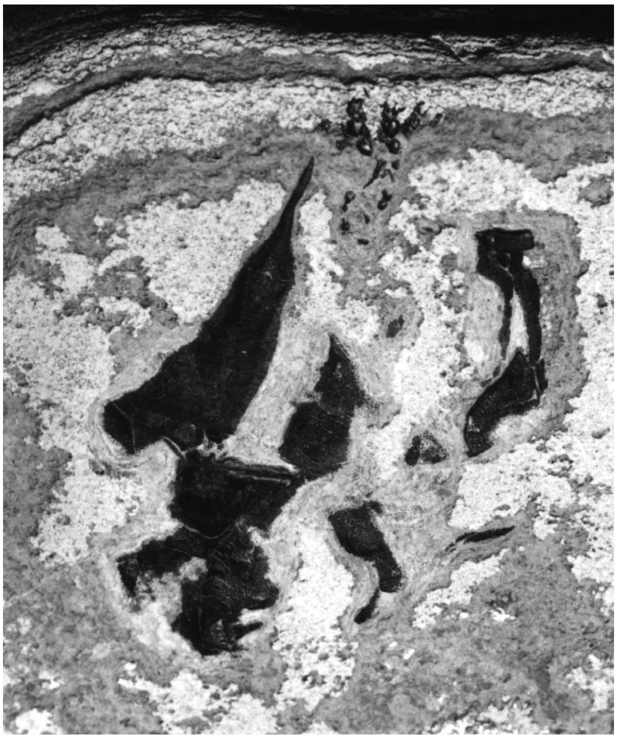


Plate 2

C. 369 [after preparation]

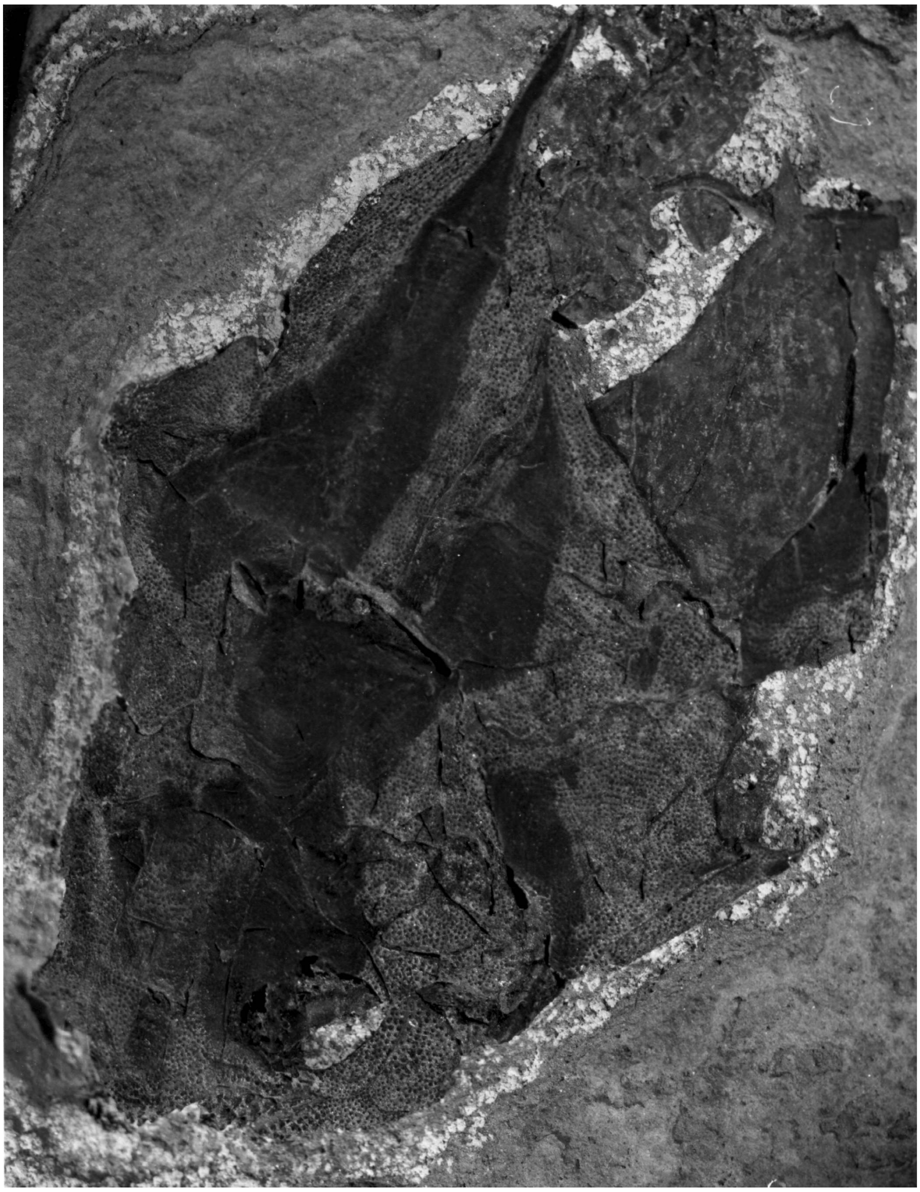


Fig. 1

***Millerosteus minor* UCL specimen C. 369**

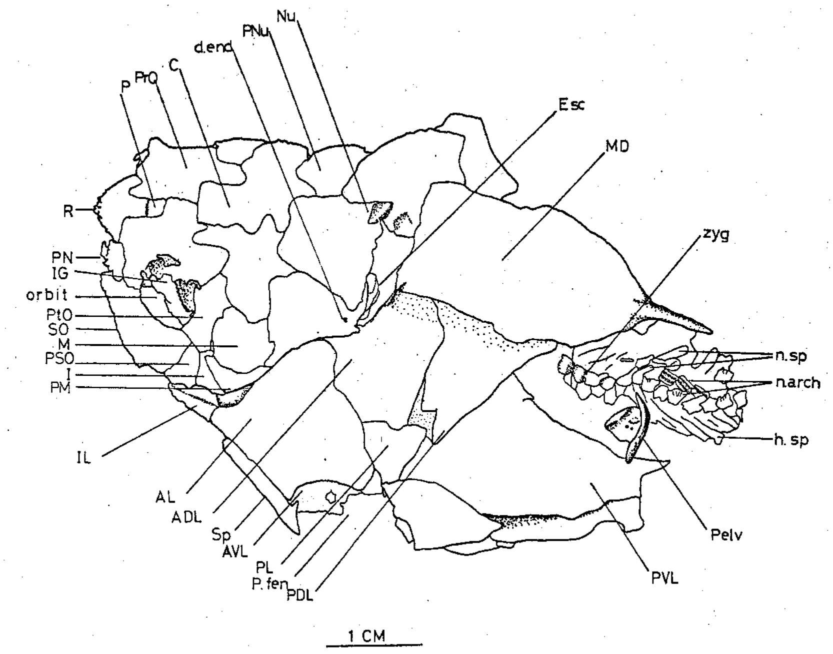


Fig. 2

[C. 369 head shield showing sensory canals]

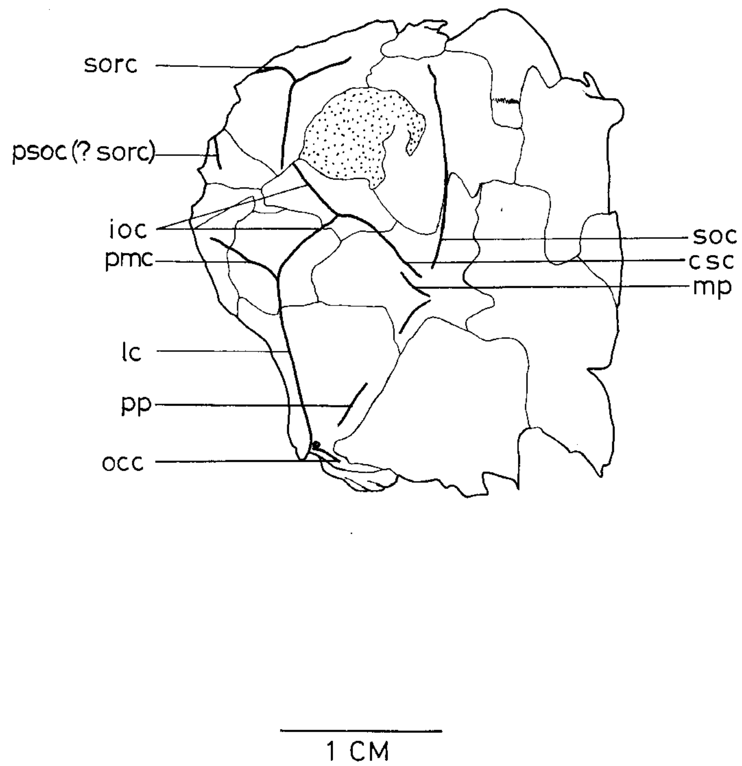
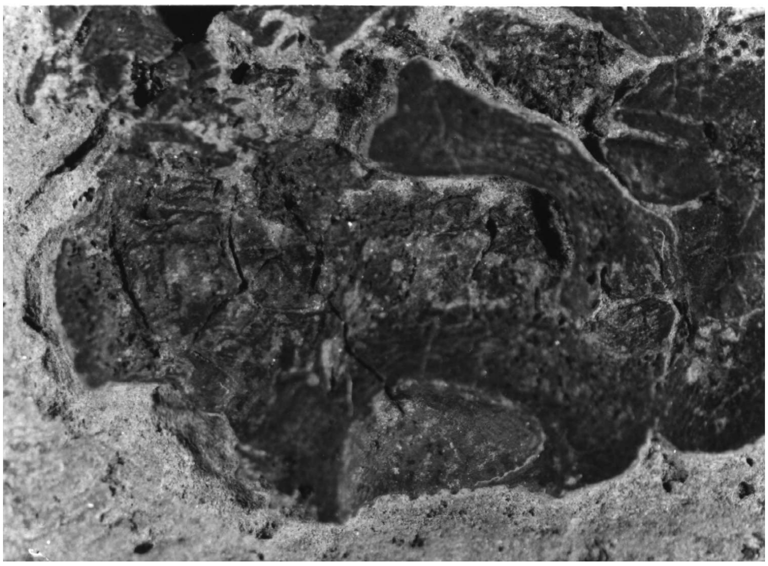


Plate 3

C. 375 after preparation



before preparation

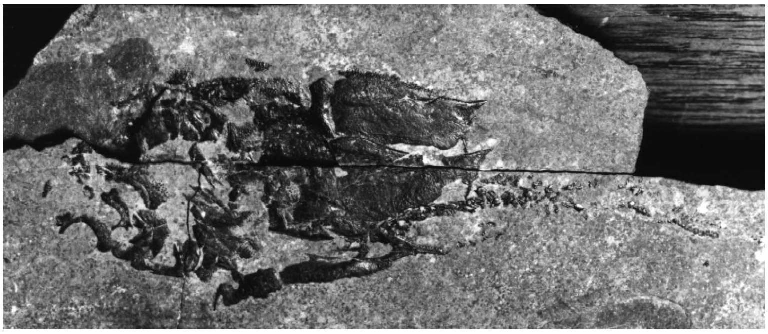


Fig.3

C. 375

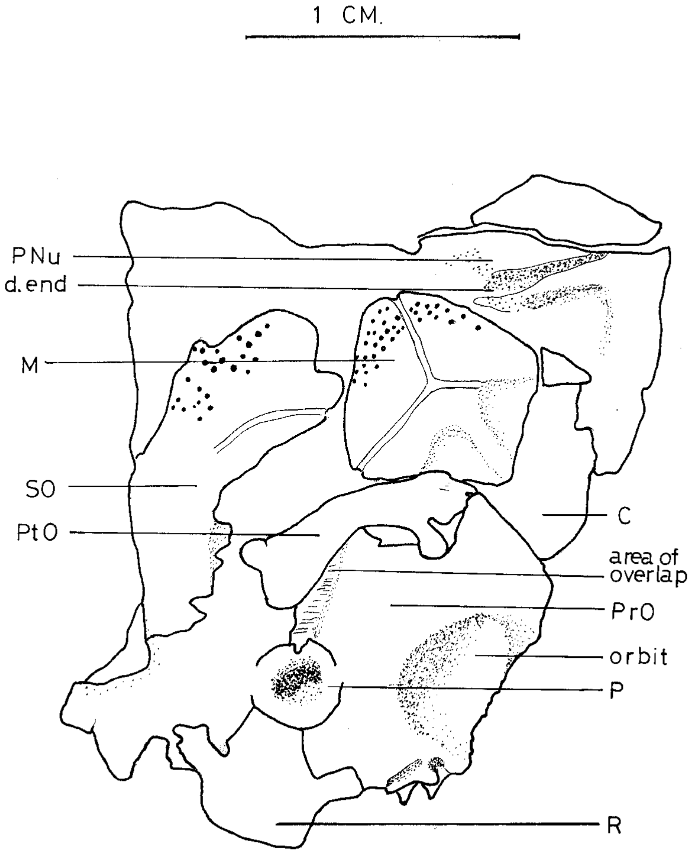


Plate 4

C. 353

Fig. 4

C. 353

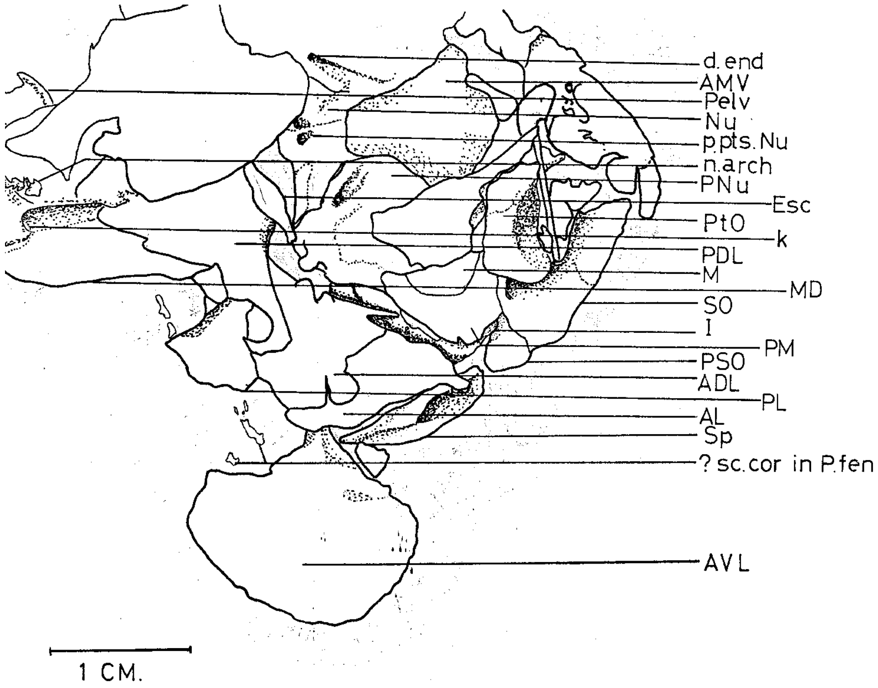
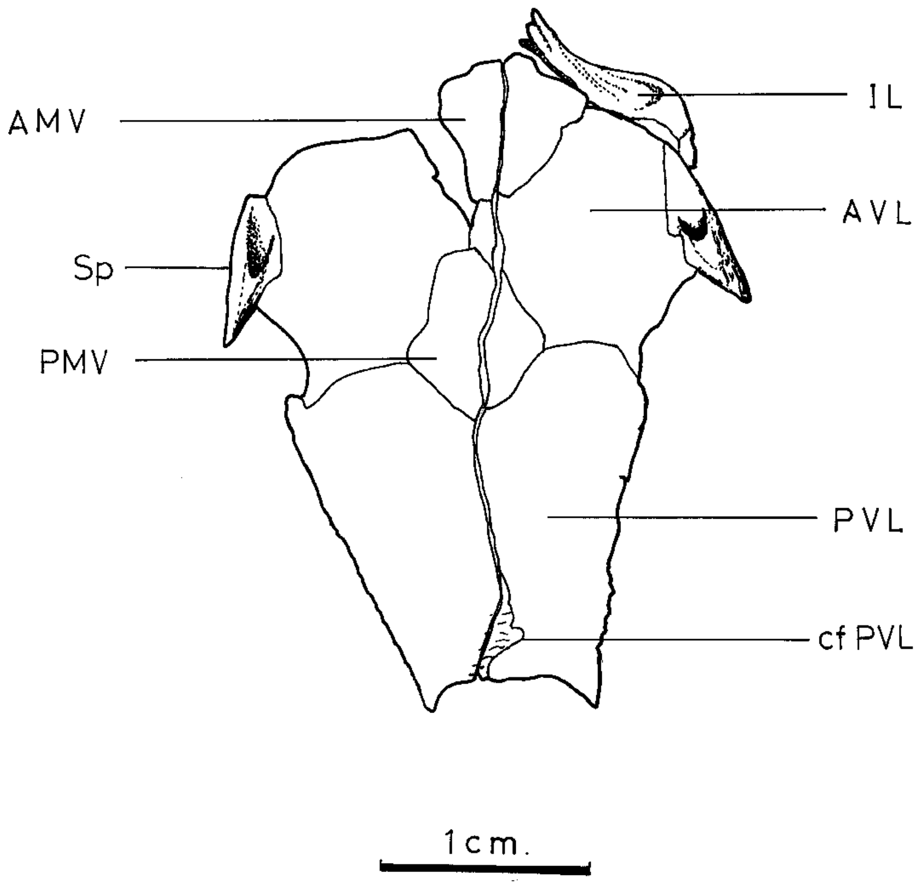

d.end
AMV
Pelv
Nu
p.pts.Nu
n.arch
PNu
Esc
PtO
k
PDL
M
MD
SO
I
PM
PSO
ADL
PL
AL
Sp
? sc.cor in P.fen
AVL
1 CM.

Plate 5

C. 349

Fig. 5

C. 349



The C. 369 *Millerosteus minor* is a large specimen (the median dorsal being 32.5 mm long, whereas the largest recorded, as reported in Miles and Westoll (18), is 35 mm) which is seen in dorsal aspect (plate 2). The entire dorsal surface of the head and trunk shield is visible and the left cheek and left thoracic dermal bones are complete and visible. The visceral surface of the posterior ventral plates may be seen as well as the anterior region of the vertebral column. In C. 353 (plate 4) the visceral surface of the dorsal region is visible, while C. 375 has been prepared to show the visceral surface of the dorsal bones of the snout (plate 3), the visceral surface of the dorsal plates and external surface of the ventral plates are also visible. C. 349 displays the visceral surface of the ventral thoracic armour (plate 5). Other (disarticulated) specimens, where they display certain characteristics or plates well, will be used in the ensuing description.

The dermal armour of C. 369 measures 66 mm long, from the rostral bone to the tip of the dorsal spine (cf. an average of 150 mm for *C. cuspidatus*). From the rostral to the posterior end of the nuchal is 29.5 mm, while the median dorsal is 32.5 mm. (As in *C. cuspidatus* about 45% of the length of the armour is occupied by the head shield and just under 50% by the trunk shield.) The extrascapulars (which have come to be overlapped by the nuchal) and gap between the head and trunk armour account for the difference of 4 mm. The total length of the armour of C. 353 is less than 58.5 mm (the rostral is disarticulated and has moved anteriorly), while C. 375 is 64 mm. The total length of *Millerosteus* is unknown, although C. 336 has a vertebral column stretching over 50 mm posterior to the dermal plates (but the latter are undoubtedly disarticulated and so of little value quantitatively). In *C. cuspidatus* the unarmoured part of the fish posterior to the median dorsal plate is equal to 2.8 times the length of that plate; if this were the case for *Millerosteus* the unarmoured region of C. 369 would have been 91 mm and the entire fish 157 mm.

Morphology of the dermal head shield

Figs 1 and 2 shows the external surface of the exoskeletal skull roof and cheek region of C. 369; fig. 3 shows the visceral surface of the skull roof only of C. 375, whilst fig. 4. shows the visceral surface of C. 353, in which may be seen both the skull roof and cheek region (see plates 2, 3, 4). The dermal bones, which are tightly locked together by overlapping margins and sinuous sutures (except the extrascapulars which apparently were loosely embedded in the skin and so easily lost), comprise three median bones in the skull roof: the rostral (R), pineal (P) and nuchal (Nu) plates. Lateral to these on the skull roof are the paired postnasal (PN), preorbital (PrO), postorbital (PtO), central (C) and marginal (M) plates, with the paired extrascapulars (Esc) posterior to the nuchal. The cheek region comprises three plates posteriorly: the postmarginal (PM), submarginal or, perhaps more correctly since it is not in contact in *Millerosteus* with the marginal, the internal (I), and postsuborbital (PSO). Anterior to these and ventral to the orbit is the suborbital (SO) plate.

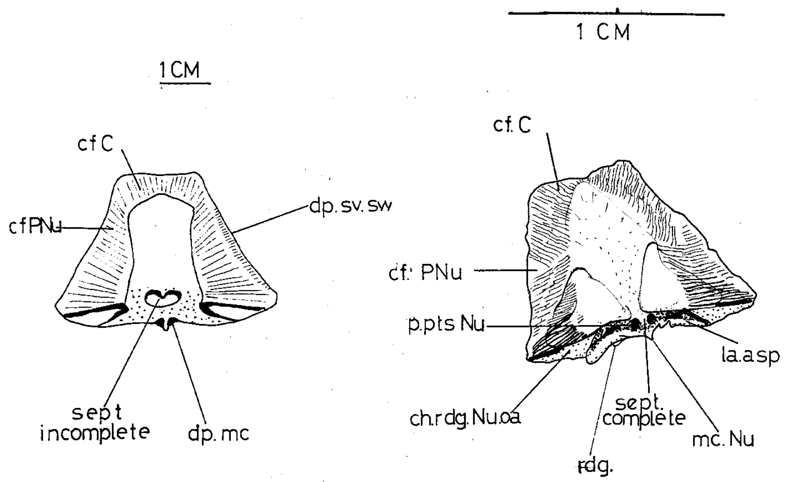
The nuchal plate (fig. 1 external surface, figs 4 and 6 visceral surface; fig. 6 is C. 362, a disarticulated nuchal seen in visceral view). Posteriorly this plate is convex shaped and anteriorly a median cusp is present. In *C. cuspidatus* there are depressions (dp.mc) lateral to this cusp when seen in visceral view, whilst in *Millerosteus* these are not visible. There are, however, ridges (rdg) more laterally and a depression between them and the cusp. If these depressions are equivalent to those in *C. cuspidatus* then they may be seen to be much more expanded laterally in *Millerosteus*. The nuchal overlaps both the paranuchals and centrals, but the contact surface with the latter differs greatly from that seen in *C. cuspidatus* (fig. 6). In *Millerosteus* the contact surface is not complete anteriorly, as it is in *C. cuspidatus*, but only occurs laterally, the exposed visceral surface of the nuchal reaching the anterior border of the plate. As in *C. cuspidatus*

Fig. 6

C. cuspidatus redrawn from Miles and Westoll (18)

M. minor specimen C. 362

Visceral Surfaces



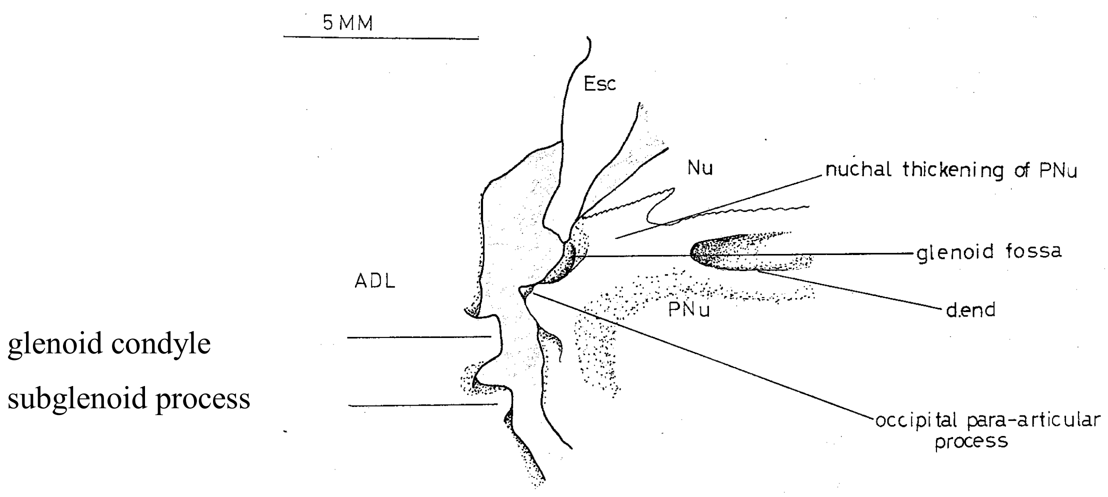
cf. differences in contact surfaces, pit septs, post. depressions and dp.sv.sw

depressed areas for the reception of the ridges of the paranuchal are present along the posterior edge of the nuchal (ch.rdg.Nu.oa), although the depression on the lateral contact surface of the nuchal for the supravagal swelling on the paranuchal (dp.sv.sw) cannot be seen in *Millerosteus*. In the posterior exposed region lie a pair of pits (p.pts.Nu), more posterior in *Millerosteus* than in *C. cuspidatus*. These lie in a depression and are completely divided by a septum (sept) in both specimens C. 362 and C. 353 in which it is visible, although this is not always so in *C. cuspidatus.* Stensiö (19) reconstructs this latter coccosteid without a septum at all; it is depicted in Miles and Westoll (18) as present but incomplete. It is interesting to note that it is complete in the juvenile *C. cuspidatus*. Stensiö (19) believes these pits were the area of insertion of the tendons of the paired levator muscles of the head. Posterior to these pits there is, in *Millerosteus*, a well-defined lamina ascending to the skull roof (la.asp) in which are situated the wide depressions already alluded to. Growth rings on the external surface of C. 369 indicate that the juvenile *Millerosteus* had a less markedly concave anterior border to the nuchal, although it was not convex as it was in the young of *C. cuspidatus*.

The paranuchal plate (external surface figs 1, 10c; visceral surface figs 4, 7) borders the nuchal central, marginal and, despite Stensiö's incorrect restoration (fig. 25) about which more later, the postmarginal. The paranuchal is thickened posteriorly and laterally where it borders the nuchal (nuchal thickenings of the paranuchal, Stensiö (19)). It underlies the nuchal plate, as may be seen from the contact faces on the visceral surface of the nuchal and the overlap area on the paranuchal (fig. 10c). Anterodorsally it stops short of the nuchal's anterior most margin, as noticed by Heintz (20) but incorrectly figured by Stensiö (fig. 25). Posterodorsally the nuchal bears a postnuchal process (fig. 1). This is thought by Miles (1962) to provide a brace for the paranuchal which, in the Brachythoraci, bears a deep glenoid fossa for articulation with the condyle borne on the anterior dorsolateral. Fig. 7 shows the visceral surface of the exoskeletal cervical joint in which

Fig. 7

C. 353 exoskeletal cervical joint



may be seen the glenoid fossa; this articulates with the glenoid condyle on the anterior dorsolateral. The fossa is sculpted out of the nuchal thickening of the paranuchal. Lateral to the fossa there is the occipital para-articular process, which seems to have two projections: the one figured arises from the basal layer of the bone (as in *C. cuspidatus*) although in *Millerosteus* there seems to be a basal component, which may be seen protruding beyond the basal process in the figure. Between these two and lateral to the process as a whole lies a groove at about half the depth of the bone thickness; this receives the subglenoid process of the anterior dorsolateral when the head is depressed maximally.

Posteroventrally the paranuchal is overlapped by the posterior dorsal lamina (pdl, fig. 9a) of the marginal; this lamina is not shown in Stensiö's restoration (fig. 25, cf. figs 9a, 10c). Anterior to this the paranuchal overlaps the marginal. See below for paranuchal/postmarginal relationship.

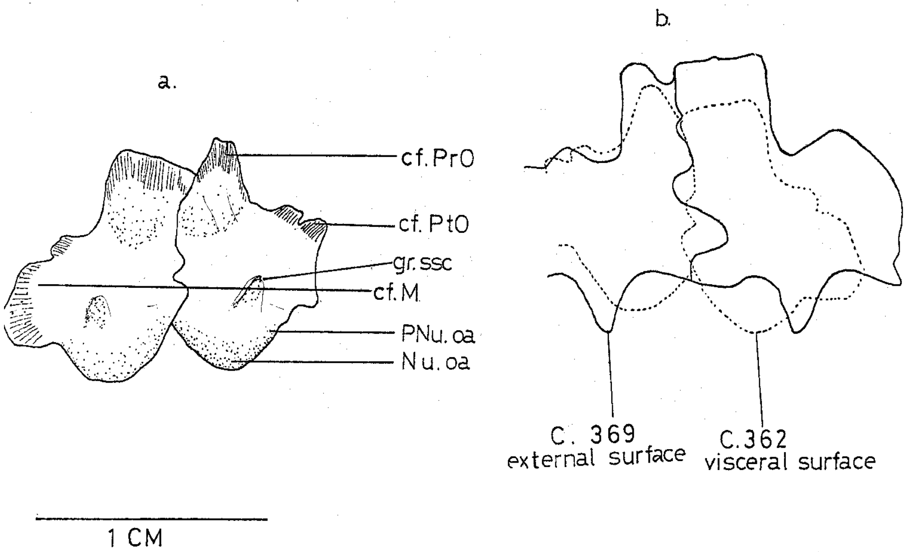
Across the external surface of the paranuchal plate runs the very deep sensory canal in an anterolateral direction towards the marginal. On the dorsal surface the posterior pit line occurs as a shallow sulcus parallel to the nuchal, only being visible in places. Whereas in *C. cuspidatus* the pit line becomes a deep groove towards its union with the main lateral line canal at the posterior end of the paranuchal, so that it may be seen to be a branch of this canal, in C. 369 this cannot be seen, the pit line only becoming visible anterior to the opening of the ductus endolymphaticus (fig. 2). This pit line can be traced onto the central plate. The occipital cross commisure is very difficult to observe but in C. 369 it is probable that it is represented by a shallow groove immediately posterior to the external foramen of the ductus endolymphaticus – this, however, is not at all certain. In *C. cuspidatus* it is also a very variable feature. The endolymphatic duct (d.end, figs 1, 2, 3, 7) traverses the lateral nuchal thickening internally, appearing as a foramen on the surface of the paranuchal plate near the cervical joint (C. 369). The duct may be followed viscerally, for in both specimens (C. 375, C. 353) in which it is visible the floor of the channel has broken away leaving a deep groove.

In *Millerosteus* the paired central plates (external surface fig. I, visceral surface fig. 8a) are not so sharply divided into anterior and lateral lamellae as they are in *C. cuspidatus* (the distinction is quite blurred in C. 362, fig. 8), although it was noted by Miles and Westoll (18) that a small minority of the latter do possess centrals without this notching, ie. of the characteristic *Millerosteus* shape. Fig. 8 shows a pair of disarticulated central plates which have remained locked together by the 'median' suture which, although comparatively straight viscerally, is quite sinuous externally (figs 1, 8a & b). When viewed externally or viscerally the right plate of the pair is seen to be larger than the left, although this probably fluctuates among individuals, as in *C. cuspidatus*. Posteriorly the centrals overlap the nuchal (see fig. 6) and the exposed V shaped visceral surface of the nuchal which approaches the margin of the plate (cf. *C. cuspidatus*) fits well into the V-shaped boundary of the paired centrals. The centrals are also overlapped by the paranuchals although a short process is left projecting between the nuchal and paranuchal (as in *C. cuspidatus*). In fig. 8 may also be seen the contact faces on the centrals for articulation with the pre- and postorbitals, both of which are overlapped by the centrals. Also on the visceral surface a small groove may be seen (gr.sse); this is to receive the semicircular canal ridges. This groove differs markedly from that in *C. cuspidatus*; in the latter it is an open V shape, while in *Millerosteus* it is a straight groove.

The external surface of the centrals of C. 369 bear two sensory lines, the supraorbital and central sensory canal (fig. 2), but on these plates neither are deeply furrowed as they are in *C. cuspidatus*; in *Millerosteus* it is only when these canals cross to the post- and preorbitals that they become deeply grooved. In fact both canals have the appearance of a shallow sulcus, of the same depth as the middle and posterior pit lines. In *C. cuspidatus* these canals typically meet, although in the C. 369 *Millerosteus* the supraorbital canal stops well short of the central canal. Heintz (20)

Fig. 8

C. 362 Centrals visceral surface



cf. outer and inner sutures

NB. There is a difference in size between these two specimens which are both drawn to the same scale.

recorded this and Stensiö (19) figured it in his reconstruction of *Millerosteus* (reproduced as fig. 25) so it is probably a fairly consistent feature. It is also known to occur in *C. cuspidatus*. In C. 369 the supraorbital canal passes across the anterior end of the lateral border of the central plate onto the pre-orbital (fig. 2) – not the anterior border, as is believed by Stensiö. The posterior and middle pit lines do not meet in C. 369, or in Heintz' specimens, although they approach one another fairly closely dorsally. The middle pit line, which is only 2 mm long, is almost straight and lacks the dorsal curve anteriorly which it possesses in *C. cuspidatus*. Anteriorly the posterior pit line in C. 369 does not curve dorsally as much as is represented by Stensiö's diagram, or as in *C. cuspidatus*, although it is probable that these pit lines are subject to a great deal of variation.

The anterior border of the centrals, where they overlap the preorbitals, are seen in Stensiö's reconstruction to be both V-shaped, yet in both C. 369 and C. 362 one of the plates (the right one in both instances) is squared off. This is probably coincidence and this is probably another example of a fluctuating feature.

The marginal plate (external surface fig. 1, disarticulated fig. 3; visceral fig. 4, redrawn fig. 9) seen in external view has the main lateral line canal pass onto it posterolaterally from the paranuchal; this becomes the otic branch of the infraorbital canal which passes anteriorly onto the postorbital plate. At their junction they give rise to the postmarginal canal which runs ventrally onto the postmarginal plate, as in *C. cuspidatus*. The angle made by these canals differs from that seen in *C. cuspidatus*; the angle made by the infraorbital and postmarginal canals in the latter is approximately 140˚, whereas in *Millerosteus* it is only 115˚. Correlated with this there is a marked difference in the shape of this plate between the two genera, that of *C. cuspidatus* being more dorso-ventrally elongated, but narrower antero-posteriorly than *Millerosteus* (fig. 9a & b).

Dorsally the marginal underlies both the paranuchal and central (see contact surfaces fig. 9a) although it differs from *C. cuspidatus* in that the contact surfaces for the two areas of overlap are not continuous. As in *C. cuspidatus* there is a posterodorsal lamina of the marginal (see fig. 9a; oa on PNu fig. 10c) which overlaps in the corresponding recess of the paranuchal (for overall contact relations see fig. 10d). No contact surface for the postorbital plate is seen in C. 375, although it is quite probable that a small overlap area exists ventral to the infraorbital canal (this would appear to be the case in C. 369). On the visceral surface of the marginal is seen the crista inframarginalis, a well developed ridge visible in C. 353.

Stensiö (1963) (19) has reconstructed *Millerosteus* (fig. 25), basing it on the plates and figures published by Heintz (1939) (20). In the text Stensiö notes:

> "In *Coccosteus*, *Pluordosteus* and *Millerosteus* where it is still an independent bone, the dorsal preopercular plate (pop_1) [here termed the postmarginal] is as a rule separated from the paranuchal plate by the marginal (M) which usually stretches backwards here right to the anterior margin of the exoskeletal skull roof." p. 226

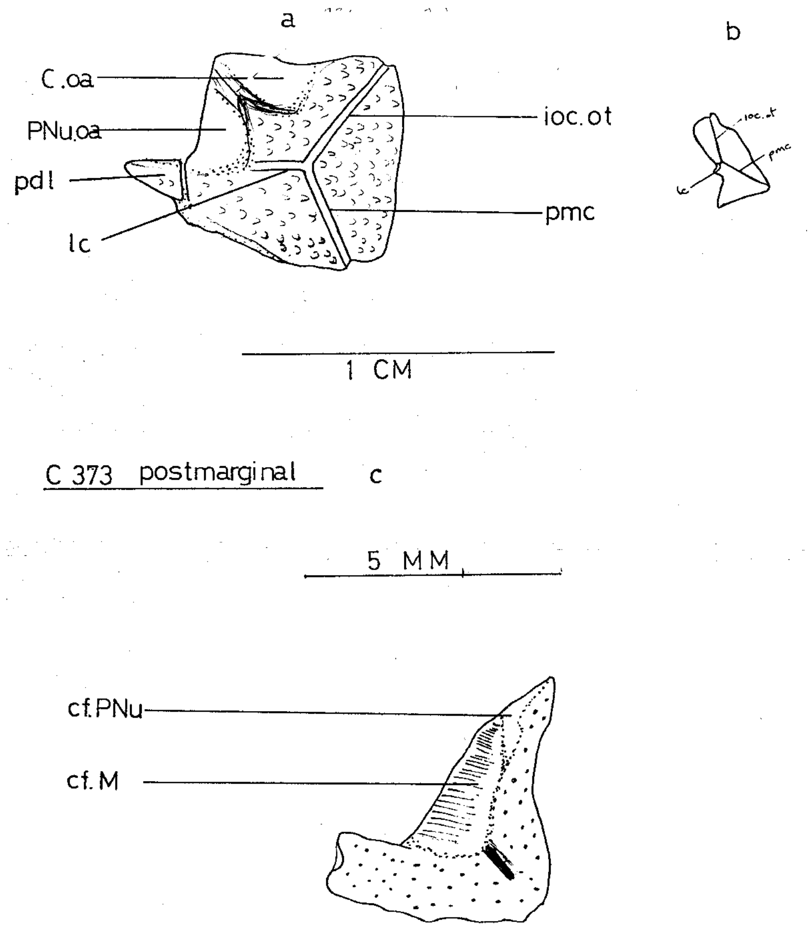
Of Heintz' two figures of the complete head shield of '*C. minor*', one is, indeed, as Stensiö figures it, but the other clearly shows the postmarginal in contact with the paranuchal (EB of Heintz, fig. 2, p. 5). Heintz notes in the text that:

> "The development of the PM plate is interesting, it is much larger than in *C. decipiens* and comes in contact with M, PtO *and EB (PN)*". p.4 (my emphasis)

Clearly he realised that the first specimen was atypical; it is possible that the anterior margin of the anterior lateral plate is obscuring the postmarginal/paranuchal junction. The meeting of the latter plates is clearly seen in C. 369 (fig. 1, 10a, b and overlap relations d [see Plate 7]), as well as other specimens in which this region is visible (visceral surface of C. 353, fig. 4) and an isolated PNu/M/PM complex, BM(NH) spec. no. P 6510. Stensiö is thus incorrect in his statement above as regards *Millerosteus*, and Miles and Westoll have shown it to be untrue for *C. cuspidatus* as well. In C. 369 the paranuchal plate,

Fig. 9

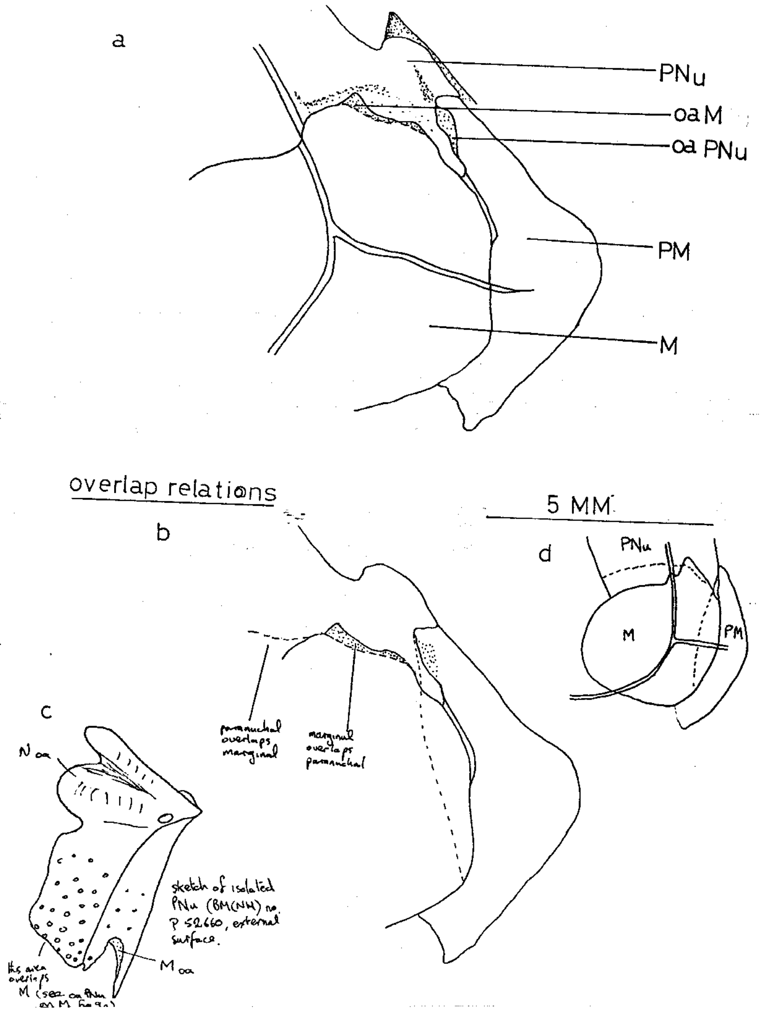
C. 375 right marginal



b. *C. cuspidatus* – redrawn from Miles and Westoll (18).

Fig. 10

C. 369 PM region



c. sketch of isolated PNu, BM(NH) no. P52660, external surface (cp overlap on PNu on M fig. 9a).

d. diagrammatic representation of cheek margin and overlap relations.

lateral to the marginal, overlaps the postmarginal plate. The postmarginal and paranuchal plate boundaries meet obliquely and the postmarginal rises dorsally posterior to the paranuchal (fig. 10). These features may be seen more clearly in the isolated postmarginal plate C. 372 (fig. 9c) where the exposed external surface of the postmarginal forms a postero-dorsal projection, posterior to the contact faces for both marginal and paranuchal; these contact faces are clearly seen.

It is obvious from the present study that the marginal is not at the posterior border of the head shield, but rather is flanked by the interlocking paranuchal and postmarginal plates. This brings *Millerosteus* back to the position now also known to occur in *C. cuspidatus*, and the overlap relations in the two genera are very similar (fig. 10d).

The postmarginal plate (as first noted by Heintz (20)) is much larger relatively than its counterpart in *C. cuspidatus.* Unlike the latter, where the postmarginal is almost entirely posterior to the marginal, in *Millerosteus* it flanks the marginal anteriorly as well, rising dorsally to make sutural contact with the postorbital. Also the postmarginal canal turns forwards upon reaching the postmarginal in *C. cuspidatus*, whereas in the *Millerosteus* C. 369 it turns slightly posteriorly. (Stensiö's reconstruction (fig. 25) is incorrect; he would have it turning anteriorly, as in *C. cuspidatus.*) But, as before, with only one specimen of *Millerosteus* with this region exposed, this may turn out to be a fluctuating feature and C. 369 may not be representative.

The postorbital plate (external view fig. 1, visceral view fig. 3) of *Millerosteus* is very dorsoventrally elongated, unlike its counterpart in *C. cuspidatus*, where it is anteroposteriorly expanded. In *Millerosteus* this condition has been brought about by the greatly reduced area occupied by the suborbital plate in the cheek region. The suborbital in *C. cuspidatus* is very deep posteriorly, forming a large part of the surface area of

the cheek and also forming both the ventral and part of the posterior margin of the orbit; a great deal of the antero-posterior length of the suborbital in *C. cuspidatus* is posterior to the orbit. In C. 369 the suborbital does not project posteriorly past the level of the orbit (see restoration of cheek region, fig. 15) and consequently the postorbital is elongated ventrally to occupy the region that the dorsal part of the postorbital lamina of the suborbital occupied in *C. cuspidatus*. The shape of the postorbital plate is quite unlike that in Stensiö's restoration (fig. 25). It does not exhibit such a great ventral extension past the lower edge of the orbit as Stensiö believed; indeed Stensiö would have the plate projecting ventrally past the most ventral point of its orbital face by 1/3 of its entire length, whereas the true figure is only 1/7 of its length.

The ventral boundary of the postorbital plate in C. 369 is dissimilar from that seen in Stensiö's restoration, having only two, nearly straight, edges (Stensiö shows curved surfaces with four edges, cf. figs 1 and 25). The anteroventral edge, overlapped by the suborbital, has a greater length of margin in contact with the suborbital than does the postorbital in *C. cuspidatus* (fig. 15) Ventrally the postorbital overlaps the internal or sub marginal plate, although the postsuborbital has no contact with the postorbital at all, as shown in Heintz' text-figs 1.1, 2.2, although his text-fig. 2.1 does show a contact between these plates (20). Stensiö adopted the latter and thus perpetuated the error (fig. 25).

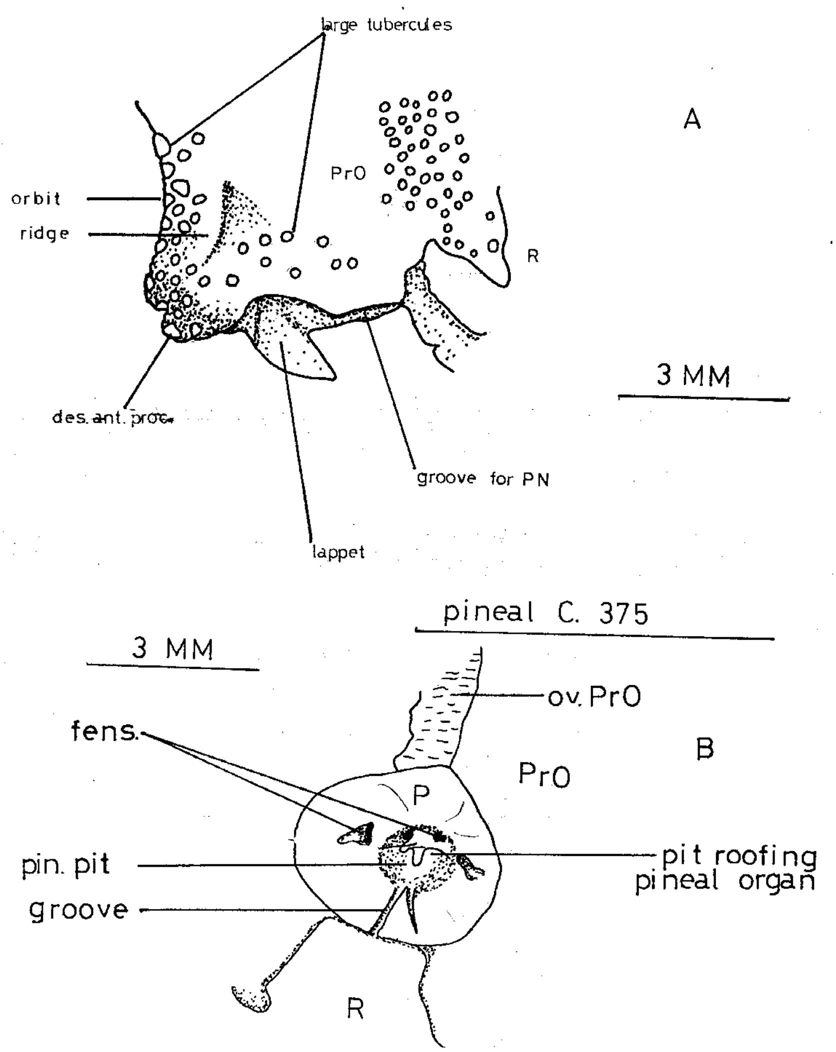
The posteroventral edge of the postorbital overlaps the postmarginal (the overlap surfaces may be seen on C. 375 (fig. 3) where the visceral surface of the postorbital is visible). The marginal plate overlies a large part of the length of the posterior border of the postorbital. Dorsally the postorbital plate is overlapped by the central and preorbital plates.

The external surface of the postorbital plate is deeply-scored by sensory canals (fig. 2). Passing onto this plate from the marginal is the otic branch of the infraorbital canal (ioc.ot). This divides after only a very short distance into the central sensory canal (csc) dorsally (continuing onto the central plate where it terminates) and the postorbital branch of the infraorbital sensory canal (ioc.pt) ventrally, which continues onto the suborbital plate.

The preorbital plate (external surface fig. 1, visceral fig. 3, 11A) has a large median area of contact with its antimere externally, much more so than in *C. cuspidatus*, and in both specimens C. 369 and C. 375 the right plate overlies the left, the area of overlap being clearly visible in C. 375 (fig. 11B). Even though the right plate overlaps the left in C. 369, the latter plate appears to have a much greater surface area and the median suture is displaced well to the right of the pineal plate and median suture of the paired centrals (fig. 1). However in C. 375 (fig. 5) the median suture is to the left of the pineal plate, indicating a larger right preorbital plate; there is obviously a great deal of variation in this region. Posteriorly these plates receive the anterior median laminae of the centrals, and in this region the centrals overlie the preorbitals (see contact faces on visceral surface of paired centrals, fig. 8). There is also a median anterior recess in which is situated the pineal plate and posterior lamina of the rostral plate. In C. 375 it may be seen that the preorbital plates are completely overlain by the large circular pineal plate viscerally, ie. in external view the preorbitals overlap the pineal; this accounts for the large discrepancy in size between the visceral and external surface of the pineal plate. Anteriorly the preorbital plates overlap the rostral plate. The anterior margin of the preorbital plate possesses a groove for the reception of the postnasal. The ventral ridge of this groove expands laterally to form a deep ventral, square-shaped lappet for articulation with the postnasal bone. This interlocking device,

Fig. 11

Preorbital C. 369



which is well illustrated on plate and fig. 11A of C. 369, in which, although the left postnasal is present, the right one is missing. The rigidity of the postnasal is ensured by this and the interlocking system between it and the suborbital, which it overlaps. The preorbital overlaps the suborbital but with projections from both interdigitating in a complicated fashion (the large tubercules make the actual margins difficult to observe). In visceral view (C. 375) the preorbital, just anterior to the orbit, is seen to have a groove ending laterally in a depression, with another depression lateral to it; these are presumably for the reception of the suborbital plate.

The anterior margin of the orbit is formed from a descending lamina or antorbital process of the preorbital. Dorsally this rises well above the level of the mid line to form a ridge above the anterior half of the orbit. The supraorbital area has broken away in C. 369 but in C. 375 it is seen in visceral view where it forms a deeply recessed region for the reception of the orbit in life (fig. 3). The antorbital process and dorsal ridge bears large tubercules. The supraorbital sensory line (soc, fig. 2) follows the preorbital-central boundary for a short distance; it crosses the preorbital in places as a moderately deep groove and terminates at the anterior level of the orbit. In C. 369 the right canal is seen, however, to extend some distance further than the left.

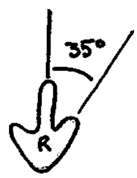
As has been seen the pineal plate (external surface fig. 1, visceral figs 3 and 11B) is much larger viscerally than externally due to the overlapping of the latter by the preorbitals and rostral. Viscerally (C. 375, fig. 11B, plate 3) the margin of the pineal plate is almost circular (it is oval and transversely orientated in *C. cuspidatus*) and in C. 375 measures from 4-5 mm in diameter. The external surface is shield shaped, not elongated rostrocaudally as in *C. cuspidatus*, and in C. 369 (which is of similar overall size as C. 375) measures 2 mm along both axes. There is thus about 1 mm of overlap area surrounding this plate.

The bone has been removed from the thin domed roof of the pineal pit of this plate in C. 369. The depression, or pineal pit, is better seen in visceral view (C. 375); here this plate is revealed as bowl-shaped, the depression which housed the pineal organs in life being posterior of the centre of the plate. At the base of the depression are to be seen a pair of pits, which, it is thought, housed the right and left pineal organs. In an attempt to corroborate the 'bilateral theory' concept of the phylogeny of the pineal organs (ie. that the present single pineal organ was preceded by two), Edinger (21) has used palaeontological evidence. She lists the occurrence of bilateral pits in *Pholidotus*, *Rhinosteus*, *Titanichthys* and *Coccosteus*, to which must now be added *Millerosteus*. Posterior to these in the mesial depression are a pair of small foramina, the function of which is unknown. There is also a pair of larger foramina, lateral to the depression, which run posteromesially following the posterolateral walls of the depression. Apparently these are so far undescribed and their function is entirely unknown. At the anterior end of the pineal plate in visceral view (fig. 11B) are a pair of grooves forming an open V-shape, with the apex directed caudally but the rami meeting the depression before joining.

The rostral plate (external surface fig. 1, visceral fig. 3) is an arrow shaped bone which is overlapped by the preorbitals and postnasals. The posteromedian lamina is longer in C. 369 than in Stensiö's reconstruction, and also relatively longer than its counterpart in *C. cuspidatus*. As with the other anterior plates it possesses enormous tubercules at its anterior margin, far larger than those of other coccosteomorphs. This plate is also of interest in that at its anterior margin it rises dorsally and then dips vertically downwards forming a pronounced right angled margin at the tip of the snout. Furthermore this anterior median descending lamina is extremely deep (almost 3 mm are visible in C. 369, and large tubercules are present even on the most ventral margin of the lamina – the significance of this will become apparent later). The angle made by the lateral laminae to the rostrocaudal perpendicular is, not 45° as Stensiö's

figure suggests, but 35°, ie. there was a greater degree of streamlining of the armour than envisaged by Stensiö. (cf figs 1, 12 and 25).

Fig. 12



The lateral lamina of the rostral is recessed ventrally, the function of which will be presently investigated.

The postnasal plate (external view fig. 1, 11A), as already demonstrated, fits into the groove on the anterior margin of the preorbital and rests on the deep lappet already described and figured, as well as overlapping the suborbital in a complicated fashion; it also overlaps the rostral although there is not a great deal of contact between these two plates. This plate is also covered with very large tubercules.

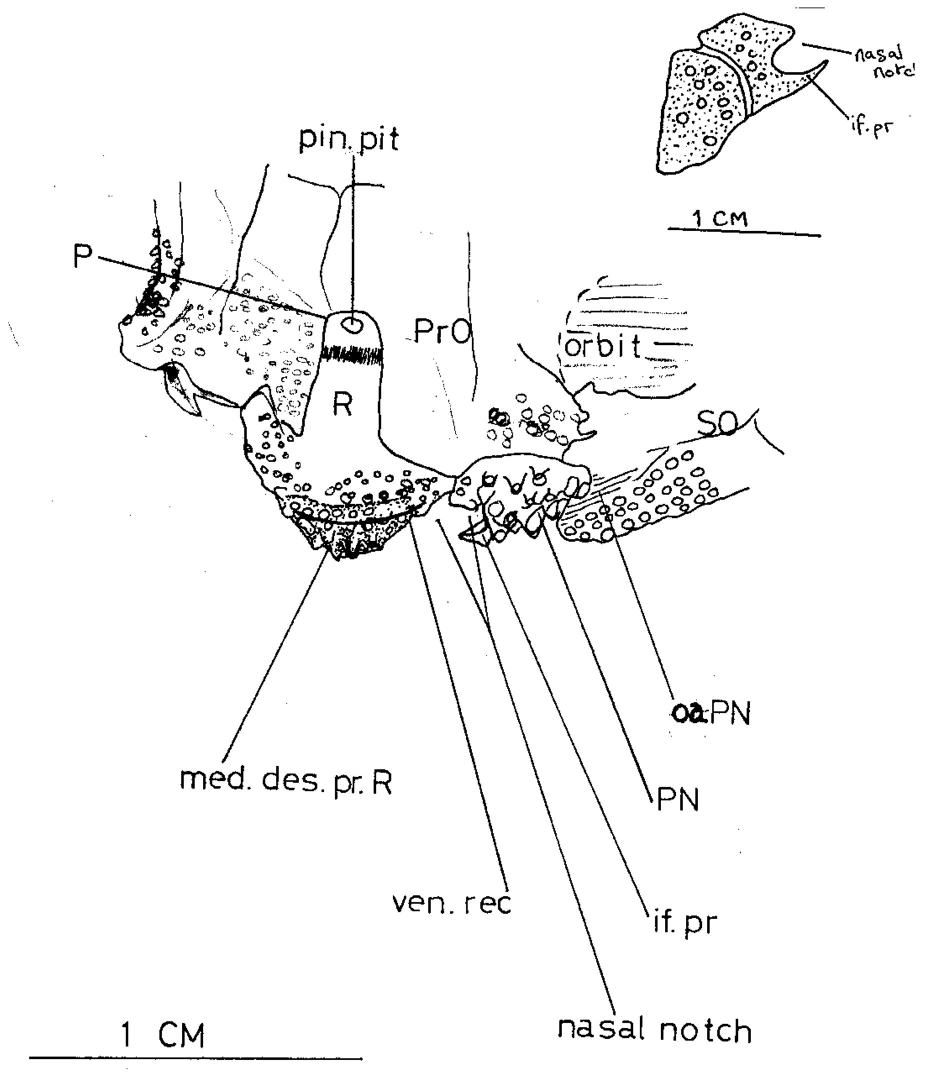
Heintz (20) noted that

> "It [the postnasal] did not show any incuts for the nostrils, known in *C. decipiens*".

yet it is demonstrable from the *Millerosteus* specimen C. 369 that there *is* such an 'incut' for the incurrent (anterior) nasal opening, formed from the recessed lateral lamina of the rostral and the deeply recessed postnasal plate. There is a prominent mesially directed ventral process on the postnasal – the interfenestral process (if.pr), exactly as in *C. cuspidatus*, where it is also broad but tapering. This process, which constitutes the ventral margin of the nostril, is believed by Stensiö to only exist in *C. cuspidatus* among coccosteomorphs, although it is frequently found among pachyosteomorphs; he states ([19] page 225) that

Fig. 13

Nasal notch of C. 369



Top right: PN of *C. cuspidatus* (redrawn from Miles and Westoll (18)). Note the similarity.

Plate 6

Nasal notch of C. 369

if.pr [indicated by line]

no such process is found in *Millerosteus minor*, and it is not shown in his restoration. Yet this process is clearly seen in C. 369 (fig. 13, plate 6). The nasal notch is thus surrounded laterally, dorsally and ventrally by the postnasal bone, and mesially by the rostral (fig. 13).

When the postnasal is restored to its presumed position in life, it encloses a large recessed hollow for the incurrent nostril, as in *C. cuspidatus*. In the latter the interfenestral process reaches across to the rostral in the restored fish, and serves to completely separate the incurrent nasal opening (fenestra exonaria anterior) from the excurrent (fenestra exonaria posterior). This is probably also the case with *Millerosteus*. The position of the nasal notch, as seen in C. 369, is shown in plate 6 and fig. 13. In the living fish this notch would have been well protected by the large tubercules on the surrounding postnasal and rostral.

Considering the facts listed below (all of which were apparently unknown to Stensiö):

a) The rostral plate has a ventral descending lamina as deep as 3 mm.
b) This lamina is covered for all of its depth with large tubercules.
c) An incurrent nasal opening is present, as in *C. cuspidatus*, and housed between the rostral and postnasal plates.
d) The streamlined shape of the anterior margin of the dermal armour.

it is impossible to accept that there was a large rostral area, anterior to the rostral plate, that was entirely cartilaginous, and that housed the incurrent nostril, as Stensiö has shown in his restoration (fig. 25). If this were the case why would large tubercules be necessary on the rostral bone some millimetres below the surface of – and thus completely encased by – the cartilage? Stensiö, in his restoration, shows only a shallow anterior margin of the rostral bone where it meets his hypothetical cartilage; he was undoubtedly not aware of the depth to which this bone actually descends or that tubercules were present on

it some distance ventrally. The function of the tubercules was probably protective and this function would have ceased if they were covered to some depth in cartilage. It is more probable, on the evidence now available, that the anterior margin of the living fish was formed of the median descending lamina of the rostral plate and laterally by the postnasal bones.

This restoration of *Millerosteus* is harmonius with that of *C. cuspidatus*, as conceived by Miles and Westoll (18). Stensiö had also restored '*C. decipiens*' with an unarmoured rostral region (see his text figure 9) stating that

> "The rostral plate [of the Coccosteomorphi] is reduced anteriorly and does not, therefore, extend forwards onto the tip of the snout" (page 225)

Yet in a footnote (page 225, note 1) he paradoxically adds that the rostral plate of *Coccosteus* may have, in fact, reached the tip of the snout, which is now known to have been the case from the studies of Miles and Westoll (18). This condition of an armoured snout must also have existed in *Millerosteus*.

The cheek region in coccosteids is composed of three plates: the suborbital, postsuborbital, and internal or submarginal. In *C. cuspidatus* these form an area of large expanse, due mainly to the enormous depth of the postorbital lamina of the suborbital (possibly 70% of the total area of this plate is postorbital in position). In *Millerosteus* it is much less well developed posteriorly, with only 20% of its total surface area being postorbital in position, although it is well developed suborbitally, relatively more so than in *C. cuspidatus*. The area occupied by the suborbital in *C. cuspidatus* is, as has already been noted, occupied in *Millerosteus* by the greatly enlarged postorbital, marginal and postmarginal, as well as by the relatively wider postsuborbital and internal. Whereas the cheek plates in *C. cuspidatus* may occupy as much as 1/3 of the total dermal armour of the head shield, in *Millerosteus* the figure more closely approaches 1/5.

Fig. 14

C. 169 Cheek region

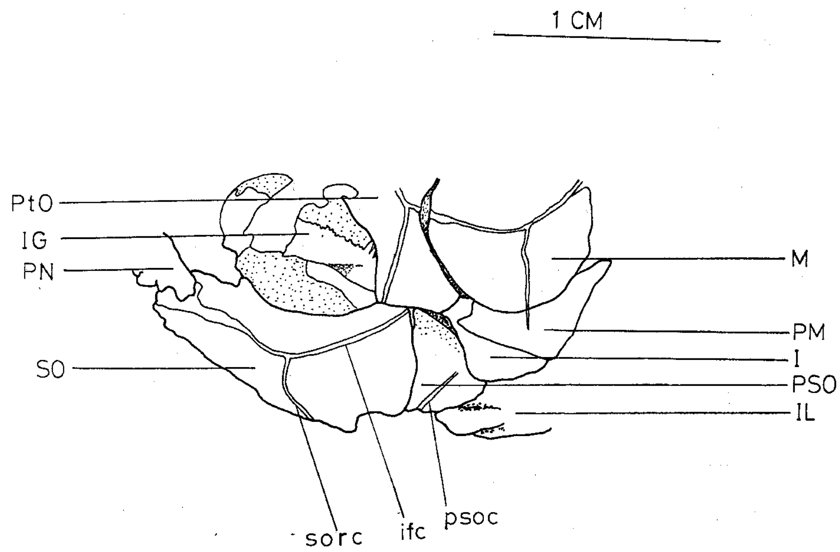
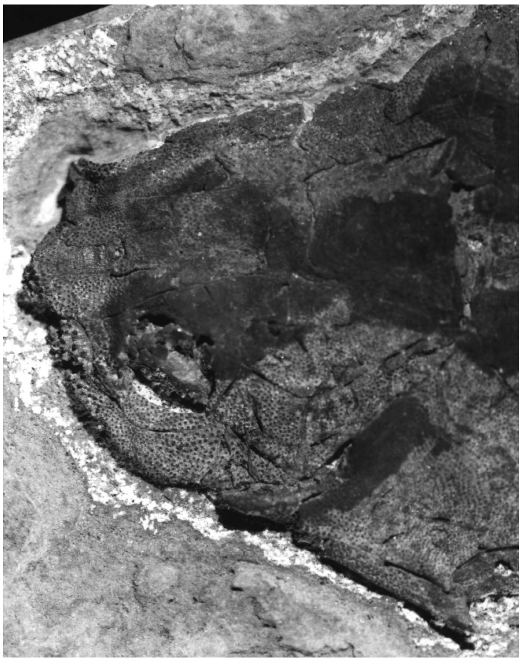
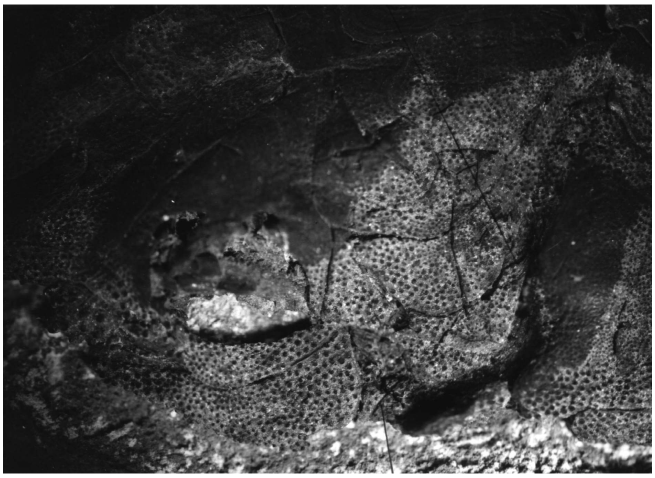


Plate 7

Cheek region of C. 368



PNu-PM contact [indicated by line]



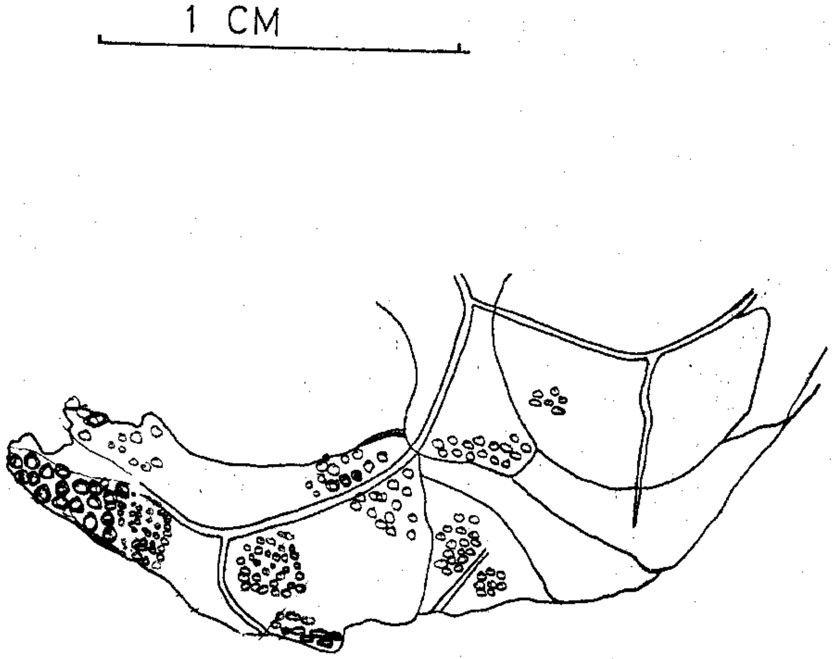
psoc [indicated by line]

The cheek unit in *Coccosteus* is only loosely attached to the skull roof, whereas Heintz (20) maintains that in *Millerosteus* it is solidly attached to the head shield. In C. 369 the cheek region has, in fact, become partially disarticulated, although the rest of the head plates are still more or less fully articulated. This is probably a measure of the distortion (flattening) undergone during fossilisation and may not indicate a more loosely attached cheek region than was previously thought. Yet there does also seem to be some disarticulation in C. 375. This must await further investigation when more complete specimens are forthcoming. If the cheek unit is, as a rule, solidly fixed to the head shield, as Heintz believes, then it is probably a consequence of the differing dermal morphology of this region in *Millerosteus*.

The suborbital plate (external view figs 1, 2, 3, 13 and especially 14; visceral surface fig. 4) is almost entirely composed of the suborbital lamina, the postorbital lamina being reduced to a very small surface area (cf. *C. cuspidatus* above). Anteriorly the postnasal and preorbital overlap this plate, the latter in a complicated manner with some interdigitation of processes. In this anterior region the tubercules are extremely large and fewer in number, becoming smaller and more numerous towards the mid region of the plate and increasing in size again towards the posterior lamina. (In *C. cuspidatus* they are of uniform size throughout.) Posteriorly this plate overlaps the postsuborbital and also the postorbital. The length of margin in contact between the suborbital and postorbital is very small and in the suborbital is restricted to the posterior dorsal edge of the postorbital lamina (fig. 14, restoration fig. 15). Stensiö shows a much larger area of contact (fig. 25), this error having arisen because he believed the postorbital to descend past the ventral margin of the orbit to a larger extent than is actually the case.

Fig. 15

Restoration of the cheek region



Towards the middle of the plate the suborbital appears bowed rostrocaudally, although the posterior end is flattened, and in life this bowing was probably more pronounced. Ventrally the suborbital is inturned along its length with large tubercules that are ventrally directed in the restored fish. This inturning finds its greatest expression at the level of the posterior margin of the orbit; at this point there is a small lappet on which is situated the foremost part of the supraoral canal (sorc). This sensory canal, which joins the infraorbital canal dorsally, is ventrally orientated before reaching this lappet, at which point it becomes caudally directed (this is not shown correctly in Stensiö's restoration). The infraorbital canal enters the suborbital plate near the dorsal posterior margin; it is farthest from the margin of the orbit in the middle of the plate, when it gives rise to the supraoral canal, after which it again rises dorsally, terminating before reaching the anterior margin of the plate. It is not seen to cross the postnasal and join with the supraorbital canal, as happens in *C. cuspidatus*.

The postsuborbital plate (external surface figs 1, 2, 14; visceral view fig. 4) is a small triangular plate in external view (C. 369) that is overlapped by the suborbital and the internal or submarginal plates. The contact surface for the submarginal is visible in C. 369 (fig. 14) and the latter plate bars the postsuborbital from contact with the postorbital, as Heintz has shown in two of his text figures (20), his reconstruction (fig. 1) and text fig. 2.2, although his text figure 2.1 shows a small area of contact of the postsuborbital and postorbital. Stensiö, who used Heintz' figures for his restoration (fig. 25), adopted the latter as the correct figure, although Heintz, in the text, makes no mention of which figure he regarded as most representative (it is telling, though, that his reconstruction shows an excluded postsuborbital). It is apparent from C. 369 that the postsuborbital is, indeed, excluded from contact with the postorbital* and the new restoration of the cheek unit (fig. 15) arising from the present study shows this accordingly. This view is lent support by study of the visceral

* This is also probably the case with a BM(NH) cast of one of Ritchie's specimens (unnumbered).

surface of C. 353 in which, again, no contact is observed. This, however, may be a variable feature, although it is interesting to note that in *C. cuspidatus* the postsuborbital is also excluded from contact with the postorbital. Stensiö's restoration must provisionally be considered incorrect, and that of Heintz correct.

Both of these authors, however, failed to notice that the postsuborbital plate bears a sensory canal, here termed the post suborbital canal (psoc), although it is probably a continuation of the supraoral canal. The postsuborbital canal, which may be seen in C. 369 (figs 2, 14), has not been described, so far, in *Millerosteus*, although it is known in *C. cuspidatus*. In the latter it completely traverses the plate, whereas in *Millerosteus* it terminates before reaching the boundary adjacent to the sub-marginal. Plate 7.

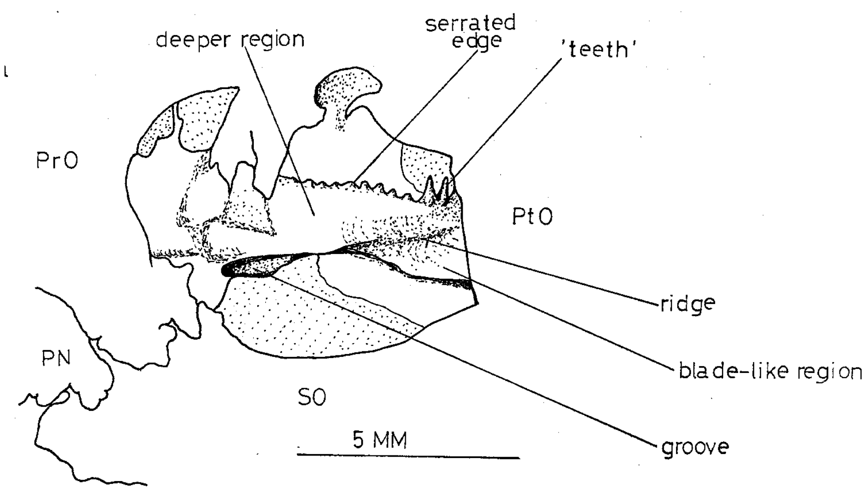
The submarginal or internal plate (external surface figs 1, 14) is overlapped by the postmarginal, and it overlaps the postsuborbital; although it reaches the suborbital it has no overlap relations with it, for a contact surface crest on the postsuborbital separates them (see C. 369). The internal is not as elongated as in *C. cuspidatus*. It is possible that some variation occurs and that the internal may stop short of the suborbital and allow the postsuborbital to have sutural contact with the postorbital, although the photograph published by Heintz showing this is too indistinct for precise determination to be made.

The lower jaw of *Millerosteus* is not well known, the main reason being that so few specimens are in existence. The only description in the literature is by Heintz (20) who figured two rather poorly and gave only the following account in the text,

> "In the orbital opening, I noticed two long and narrow bones with a row of more or less strongly developed teeth. They may probably represent the front parts of both the IG plates. As mentioned above they are very weak and narrow, more reminiscent of the IG I described in *Phlyctaenaspis acadica* ..... than of those in *C. decipiens*.

Fig. 16

Inferognathal of C. 369



> The gnathal elements in *C. minor* were apparently neither so strongly developed nor so completely ossified as those in *C. decipiens*, for which reason they are only seldom preserved in the fossil." (page 6) *

There is, however, an inferognathal bone (IG figs 1, 16; plate 7) to be seen through the orbit of C. 369. The mesial surface of this bone is visible and the anterior (dentigerous) region is caudally directed. This, then, is the left inferognathal which must have become displaced through 180° after death. The visible section of the bone measures 8 mm although neither anterior nor posterior margins are visible, the former being covered by the postorbital, the latter by the preorbital. The bone must, in fact, be about twice this length to reach from its articulation on the visceral surface of the post-suborbital to the rostral margin.

For most of its visible length the inferognathal is very narrow. At the anterior (dentigerous) end it is very flattened laterally and blade-like when restored to the vertical position. The more posterior region (Stensiö's 'non biting division') is, as in other coccosteomorphs, expanded or spatulate, and much deeper than the anterior end. This depth is achieved by the development, initiated within the dentigerous region, of a pronounced ridge mesially, overlying a ventral groove. This ventral groove, which may in the restored bone have been a hollow but enclosed tube, opens out as it becomes more dorsal on the visible (mesial) surface. In all Euarthrodires the mentomandibular ossification of Meckel's cartilage is situated mesially at the most anterior end, but midway along the length of the inferognathal it moves ventrally to emerge in the posterior region on the lateral or external surface. It is probable that the posteriorly directed oblique ridge marks the dorsal margin of the mentomandibular, tracing its position obliquely downwards before crossing under the inferognathal to the lateral surface. The function of the deep ventral groove is not known, it may be concerned with Meckel's cartilage, or with the ramus mandibularis internus VII, although it would appear rather large to accommodate the latter.

* Woodward had similarly alluded to sharply pointed teeth (4).

At about the mid region of the visible portion of the inferognathal there is a series of some 8 or 9 poorly preserved ridges, forming a serrated edge. Immediately posterior to these are visible three huge 'teeth' which have the appearance of cone-shaped spikes, undoubtedly the 'more or less strongly developed teeth' of Heintz. These stabbing 'teeth' are highly indicative of strongly predaceous habits. How many more (if any) are present in this specimen under the postorbital cannot be gauged, although attempts at detecting more have met with failure (Heintz' published photograph, shows four or five such 'teeth'). The largest of these 'teeth' in the UCL C. 369 specimen measures just less than 1 mm and is relatively far larger than those of *C. cuspidatus*, as well as being a different shape.

A search through the specimens of the BM(NH) has revealed two more partial lower jaws, one from the 19th century Peach Collection (BM(NH) specimen no. 42387) collected from Murkle Bay, and the other presented recently by J. Saxon (BM(NH) specimen no. 50158). These are here figured as sketches, made without the use of a camera lucida, as figs 16b and c).

The Peach specimen (fig. 16b) is only 4 mm long and has clearly exhibited four 'teeth' which, as observed in the UCL specimen, are enormous, perhaps as large as 0.75 mm. The inferognathal shows very little detail; it is very narrow, broken at both ends and the 'teeth' are very similar in shape to those of the UCL specimen, being elongated cones. The dimensions of the jaw are shown in the sketch.

The other jaw (fig. 16c) is much longer, 8.8 mm, again very narrow, being 1mm wide at the narrowest region and only 1.5 mm at the widest. This jaw is remarkable in the number of 'teeth' presumed to have been present in life. At one end there are four rather worn triangular-shaped cones, then a gap in which presumably another two 'teeth' were located, and then two more 'teeth', rather flattened but nevertheless recognisable. This makes a total of possibly eight 'teeth' in this specimen over a length of 4.8 mm. These 'teeth' have lengths of jaw measuring 4 mm and 2 mm on either side, while the extremity of the former region is expanded slightly.

Fig. 16. (cont.)

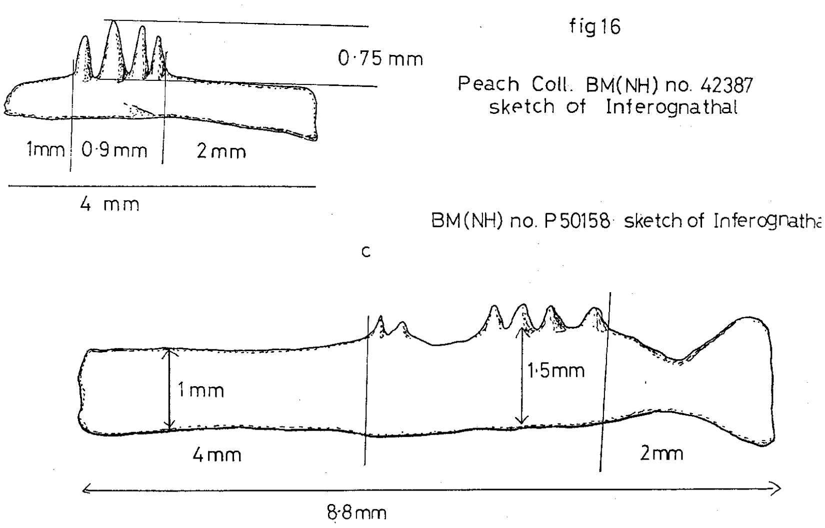


fig 16
Peach Coll. BM(NH) no. 42387
sketch of Inferognathal
0·75 mm
1mm
0·9mm
2mm
4 mm
BM(NH) no. P50158 sketch of Inferognatha
c
1mm
1·5mm
4mm
2mm
8·8mm

Morphology of the dermal thoracic shield

The thoracic armour comprises a median dorsal plate (MD), paired anterior and posterior dorsolaterals (ADL and PDL), paired anterior and posterior laterals (AL and PL); ventrally there are paired anterior and posterior ventrolaterals (AVL and PVL) as well as anterior and posterior median ventrals (AMV and PMV). Anteroventrally there are paired interolaterals (IL) and anterior to the pectoral fenestra are located the spinals (Sp).

The median dorsal plate (external surface figs 1, 17; visceral surface fig. 18), of which measurements have already been tabulated (page 26), is very slightly curved in the rostrocaudal direction, reaching its greatest height over the carinal process. Laterally the sides of the plate dip down steeply so that in transverse section the plate would be seen to be strongly arched, more so in the posterior than the anterior region. The greatest width of the plate occurs just anterior to the mid point, being caused by the plate margins becoming laterally expanded here (this is not shown in Stensiö's restoration, fig. 25). Heintz (20) believes the spine was directed upwards (as is shown in Stensiö's restoration), the rounded tip protruding through the skin in life to form a real spine (presumably just anterior to the dorsal fin). Neither the many UCL nor BM(NH) specimens studied show this so it is doubtful if the spine does curve dorsally.

The dorsal spine was extremely elongated relative to its counterpart in other coccosteomorphs, although it is rarely found unbroken in the fossil fish. In specimen C. 369 it measures a little under 1 cm. and thus accounts for between 1/3 and 1/4 of the total length of the median dorsal plate. This length is correctly depicted in Heintz' text-fig. 1.2 although Stensiö's restoration shows the spine far too short (perhaps only 1/7 of its total length). In all specimens

Fig. 17

C. 369 MD

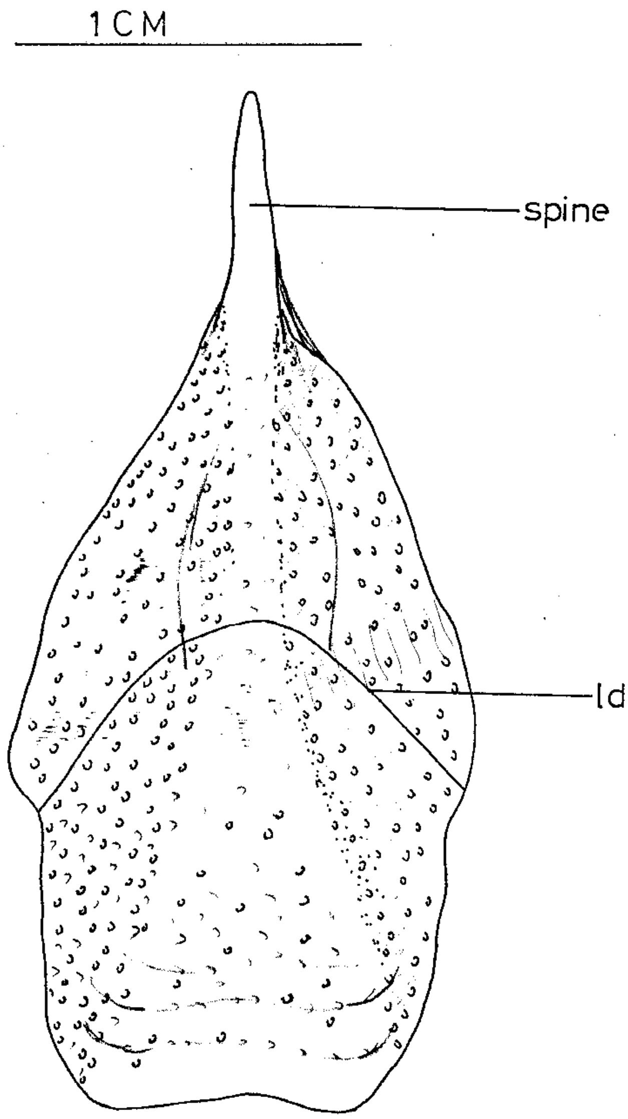
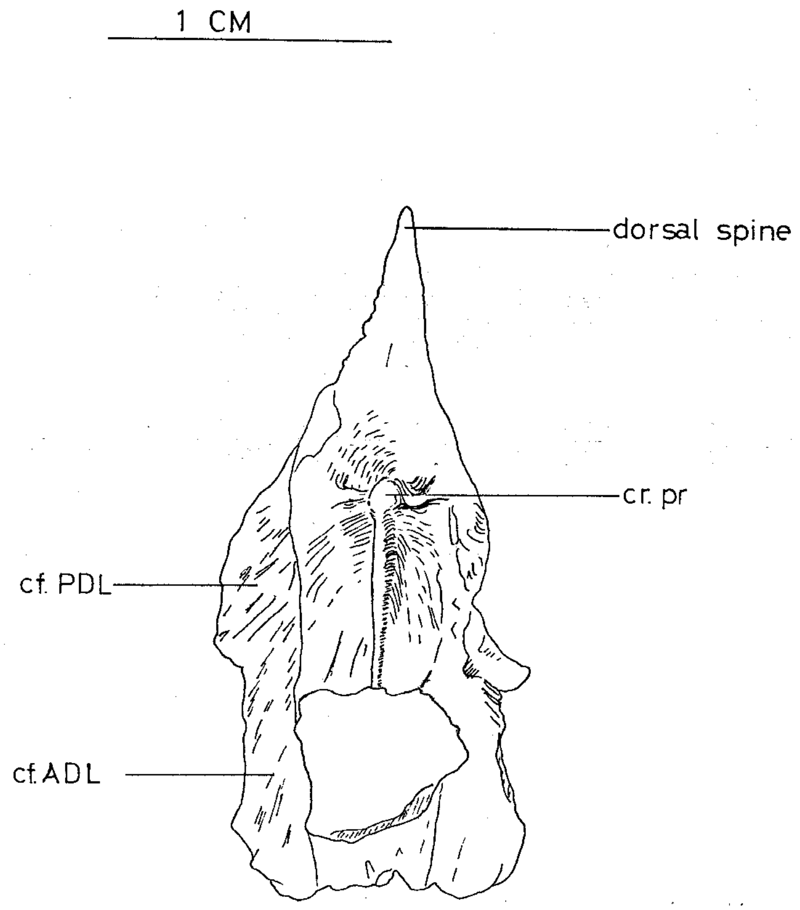


Fig. 18

C. 344 MD visceral view



examined the external surface of the median dorsal is tuberculated laterally and posteriorly although a triangular area (with its base along the anterior margin of the plate and its apex passing through the sensory line) is devoid of tubercules or has only a very few scattered over it. This does not seem to be due to erosional wear in situ as the external bone layer in many specimens is still intact. This feature is also recorded for *C. cuspidatus* and Miles and Westoll (18) suggest this region was more deeply embedded in the dermis. The dorsal branch of the main lateral line canal (ld fig. 17) crosses the plate, entering it a little anterior of centre on either side and crossing posterodorsally to meet in the mid line. (Heintz failed to notice the continuity of the groove in his specimens although, admittedly, it is difficult to observe or not present in many plates.) In most specimens the groove is shallow but most prominent on either side of the mid line, becoming inconspicuous again on the lateral margins of the plate. Miles (23; text-fig. 8B) shows this groove correctly.

On the visceral surface (fig. 18) contact faces for the overlap areas on the anterior dorsolateral and posterior dorsolateral are present, being well marked off from the remainder of the visceral surface of the median dorsal. In contrast to *C. cuspidatus*, in *Millerosteus* there is only a very low keel,* the carinal process of which is not visible in lateral view (unlike *Coccosteus*), although it occupies the same position as its counterpart in the latter. Lateral to the carinal process are a pair of anterolaterally directed ridges. The keel, although low, and the carinal process are well developed.

The anterior dorsolateral plate (external surface figs 1, 19; visceral surface fig. 7) is overlapped dorsally by the median dorsal and ventrally by the anterior lateral (the overlap areas are well exhibited in specimen C. 368, fig. 19). Anterior to the overlap of the median dorsal there lies a finger-like projection of free bone that flanks the median dorsal; similarly a larger free margin anterior to the anterolateral occurs on the ventral anterior margin when seen in external view. In the restored fish

* as in Gross's *C. cf minor* (page 26)

the suture between the anterior dorsolateral and anterior lateral rises anterodorsally for most of its length before turning sharply ventrally near the anterior margin (cf present restoration and Stensiö's incorrect restoration, figs 25, 26).* Similar projections are found in *Coccosteus*. Just posterior to this ventral projection of the anterior dorsolateral and running parallel to it there occurs on the anterior most part of the overlap area of the anterior lateral a groove to receive the dorsal part of the postbranchial lamina on the visceral surface of the anterior lateral.

The anterior margin of the anterior dorsolateral bears the dorsoventrally elongated glenoid condyle (gl.pr), and below this the subglenoid process (subgl.pr) is seen projecting from the visceral surface (see fig. 7 for relations to the glenoid fossa and occipital para-articular process of the paranuchal).

On the external surface the main lateral line canal (lc) enters the plate between the glenoid condyle and subglenoid process and passes obliquely ventrally, the canal groove being fairly deep. A dorsal branch (ld) is given off and passes dorsally before turning abruptly posteriorly**. (This is observed in all *Millerosteus* specimens, although it is an uncommon occurrence in *C. cuspidatus* where the emergence of the canal is already posteriorly directed.) As in this canal on the median dorsal it is, in some places along its length, very shallow or even not present and elsewhere fairly pronounced, if shallow. In C. 363 (fig. 19) it is quite visible when emerging from the main canal and again towards the posterior boundary of the plate, but difficult to detect in between.

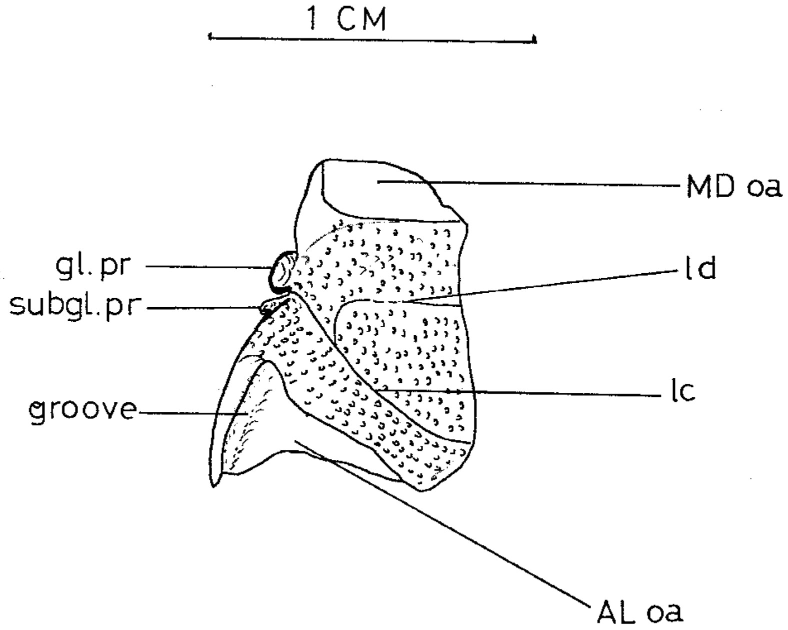
The posterior dorsolateral plate (external surface figs 1, 20a, b) is seen almost completely articulated in C. 369 (although the overlap areas to receive the median dorsal, anterior dorsolateral and posterior lateral are clearly visible). These over-

* Similarly Heintz in his text-figs 1.2, 2.1 and 2.2 fails to show this (20). It is shown correctly in Miles (23) text-fig. PC.

** Hussakof, 1911 (6)

Fig. 19

C. 369 ADL



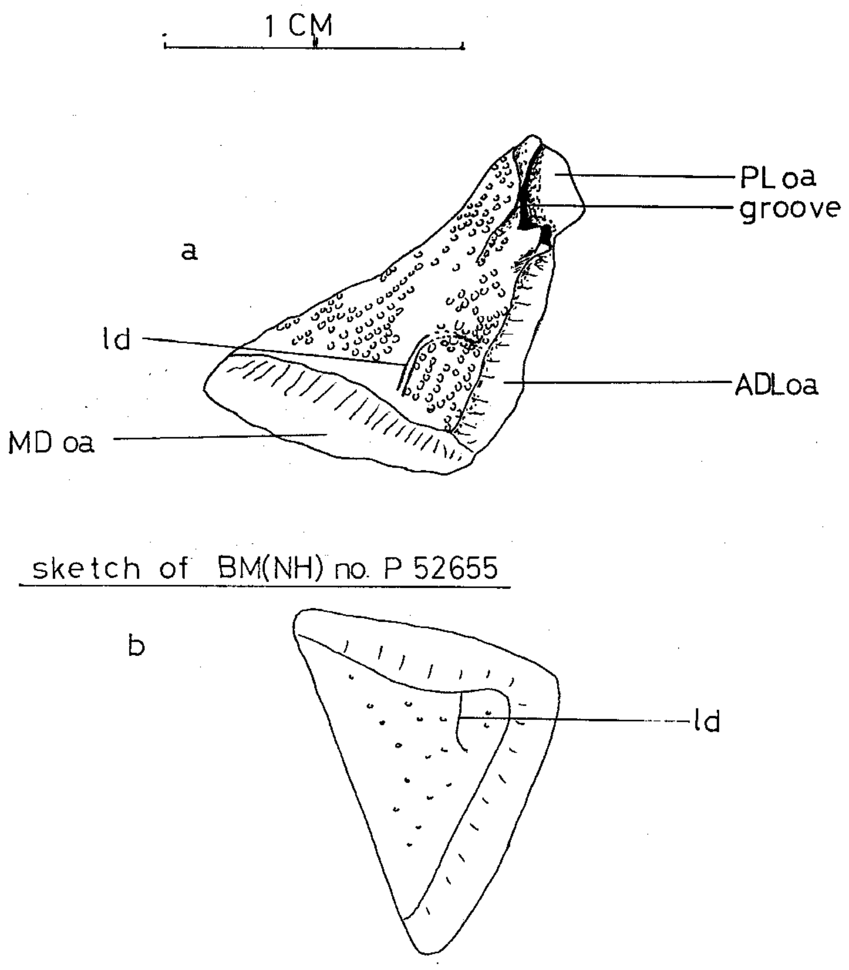
lap areas are better observed in C. 341 (fig. 20a), a disarticulated specimen. The median dorsal and anterior dorsolateral overlap areas are almost continuous, there being only a slight ridge to distinguish their boundaries, although there is a pronounced ridge separating the anterior dorsolateral and posterior lateral overlap areas for most of their length. In both C. 369 and C. 341, but better observed in the latter, there is a prominent groove, caused by the overhang of the external surface, along both the posterior and dorsal surfaces of the posterior lateral overlap surface. The posterior lateral, which obviously had a thin plate margin in this region, slotted into this groove to give a tongue-and-groove interlocking joint; this arrangement strengthened the posterior border of the thoracic armour.

Posteriorly the free margin of the posterior dorsolateral flanks the overlap area for the median dorsal and in C. 369 is drawn out into a long tapering projection, although this is less pronounced in C. 341. As in other coccosteids (eg. *Coccosteus*, *Pholidosteus*) a short projection of free plate margin flanks the posterior lateral posteriorly. (Stensiö's restoration, fig. 25, and Heintz' text fig. 1.2 (20) on which it was based, show the opposite condition, and although Miles (23) shows approximately the correct relationship, his plates have overall incorrect shapes.) For the correct shape see the present reconstruction, fig. 26.

As has been noted previously the dorsal branch of the main lateral line (ld) – which emerges from the main canal (lc) on the anterior dorsolateral and passes posteriorly to the plate margin adjacent to the posterior dorsolateral, and then is again found on the median dorsal – is only visible on these plates as a shallow groove. This is also the case for the posterior dorsolateral; although not seen on the worn surface of C. 369, it is visible on the disarticulated specimen C. 341 and also the BM(NH) specimen no. P 52655 (figs 20a, b). In *Millerosteus* this canal occurs more anterodorsally than its counterpart in *C. cuspidatus*.
The anterior lateral plate (external surface figs 1, 21a, c, d; visceral surface fig. 4) overlaps the anterior dorsolateral dorsally (see AL oa on ADL in fig. 19) and the posterior lateral posteriorly. The ventral margin forms a supraspinal lamina for most of its length (but not all); it overlaps the spinal plate and posteriorly this lamina fits a recess in the spinal (fig. 21). The anterior margin is deeply grooved, there being a ridge on the visceral surface (seen in C. 353) such that the external surface overlies the paranuchal and postmarginal when the head is

Fig. 20

PDL specimen C. 341



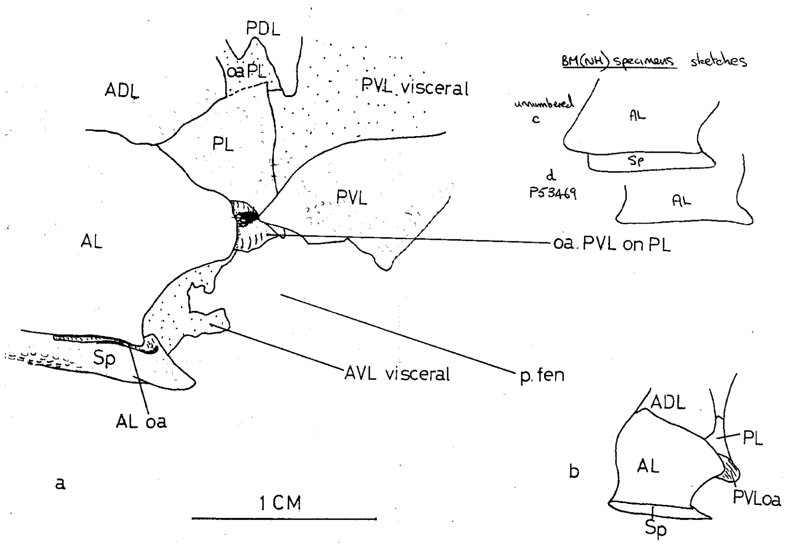
depressed. C. 369 is articulated with the thoracic overlap of the posterior margin of the head shield. There is no recess inside the postbranchial lamina on the anterior margin, although this occurs in *Coccosteus* where it accommodates the postsuborbital when the head is depressed (the different configuration of the dermal bones of the cheek make this impossible in *Millerosteus*). Although broken in C. 369, the anterior ventral corner of the anterior lateral is tapering (figs 21c, d of BM(NH) specimens). The anterior of the AL projects for some distance in front of the spinal (fig. 1; cf Heintz and Stensiö's restorations, Miles (fig. 21b) perpetuated this error – see present restoration (fig. 26)).

Posteriorly the suprapectoral margin of the anterior lateral forms the anterodorsal margin of the pectoral fenestra. In contrast to *C. cuspidatus* the anterior lateral has a relatively large length of margin adjacent to the posterior ventrolateral (best seen in C. 369 fig. 21a). The free posterior ventral margin of the AL and PL form a triangular recess, in which may be seen in C. 369 (fig. 21a) the overlap area on the PL for the PVL. This receives the dorsal lamina of the posterior ventrolateral (fig. 21). Miles' (23) text fig. 8C (reproduced as fig. 21b) is incorrect in the PL oa and the shape of the PVL/AL-PL junction generally. The margin of the PVL adjacent to the AL in C. 369 (fig. 21a), C. 370 and C. 340 (fig. 23a, b) has a complementary contour to the AL, demonstrating the true nature of the size of the contact margins between these plates and the nature of the fit between ventral and flank armour (see new restoration, fig. 26).

Anteroventrally the AL is in contact with the IL. The former plate in *Millerosteus* differs from that in *Coccosteus* in its larger ventral margin (correlated with the greatly elongated spine) resulting in a shorter pectoral fenestra.

Fig. 21

C.369 pectoral fenestra



b. redrawn from Miles and Westoll (23) fig. 8C to show incorrect Sp and PVL.oa

The posterior lateral plate (external surface fig. 21a) in *Millerosteus* is less dorsoventrally elongated than in *Coccosteus* but broader rostrocaudally, the shape being far more triangular. Dorsally this plate is overlapped by the ADL and it overlaps the PDL (oa PL, fig. 21a); the PL plate margin has a tongue-and-groove fit with the PDL. The dorsal lamina of the PL is flanked on either side by the PDL as in other coccosteids. Anteriorly the PL is overlapped by the AL and ventrally by the PVL, these two plates having overlap areas on the PL that are continuous (that for the latter is seen in fig. 21a; in C. 369 a pronounced ridge is present on the PVL oa). Miles' figure 8C (here fig. 21b) is incorrect for the PVL oa.

The spinal plate (external surface figs 1, 21; visceral surface figs 4, 5) is, relative to *Coccosteus*, a very large plate; measurements of the lengths of various specimens being as follows:

C. 369	1.25 cms
C. 353	1.2 cms
C. 375	1.05 cms
C. 348	0.8 cms

These plates occupy a length that is approximately 1/5 of the total length of the combined head and thoracic shields (cf. *C. cuspidatus* 1/7 length of armour). Although tapering posteriorly the anterior region is squared off and ends on average 1/3 cm from the anterior AL plate margin; cf. Stensiö's (fig. 25) and Heintz' incorrect figures. The mistake was repeated by Miles (23) (fig. 21b).

The posterior region projects into the pectoral fenestra some distance (about 1/5 of its length; cf. 1/7 in *C. cuspidatus*). This region is solid and in visceral view just over 1/2 of the posterior region of the plate is roofed, overhanging a cavity a short distance anteriorly, while the anterior region (just under 1/2 the total length) is open mesially with its cavity facing into the thorax. In *C. cuspidatus* the anterior 2/3 is open mesially. According to Stensiö (1959) (22) this cavity housed the lateral prepectoral process of the scapulocoracoid.

Dorsally the spinal plate is overlapped by the anterior lateral (fig. 21), ventrally it is overlapped by the anterior ventrolateral (see cf Sp on AVL, fig. 22c), the contact face on the anterior ventrolateral being much larger posteriorly. Anteriorly (fig. 5) the spinal is in contact with the interolateral. A process at the anterior end of the overlap area for the anterior lateral flanks the suprapectoral margin of the anterior lateral for a very short distance.

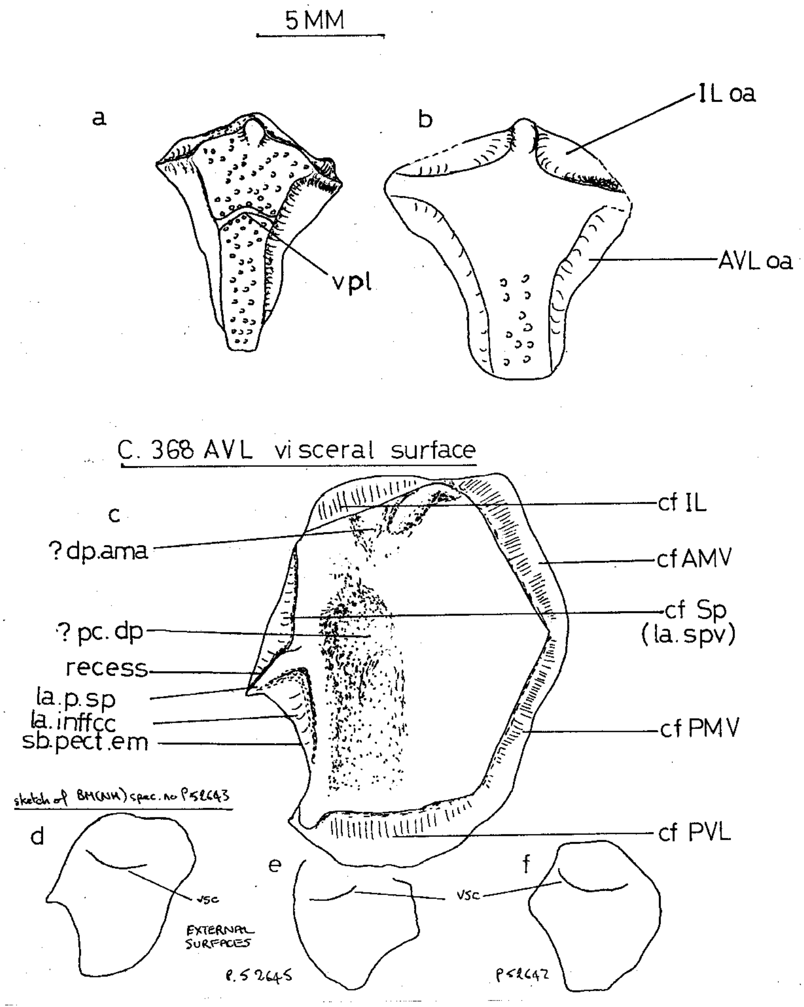
The anterior median ventral plate (external surface fig. 22 a, b; visceral surface fig. 5) is overlapped anteriorly by the interolateral, although there is an overhang of the external surface anteriorly, which often collapses, creating a groove into which the interolateral fits. The overlap areas for the right and left interolateral plates are continuous, although the median anterior projection of the free surface of the anterior median ventral restricts this junction greatly. There are lateral overlap areas for the anterior ventrolateral plates, although in C. 362, a complete and disarticulated specimen (fig. 22a), these terminate anterior to the posterior margin of the plate (C. 353, fig. 22b, is probably worn posteriorly). There seems to be some variation in the shape of the plate: C. 362 is T-shaped and elongated rostrocaudally, whereas in the articulated C. 349 the elongation is much less pronounced. Furthermore the anterior median ventral in C. 349 (fig. 5) is overlapped by the anterior ventrolaterals for its entire length, and the anterior median CANNOT have overlapped the posterior median ventral; in fact between these plates the anterior ventrolaterals themselves meet and have overlap relations, thus distinctly separating the median ventral plates. Yet the shape of the C. 562 specimen possibly indicates that the anterior median ventral fluctuated greatly in its size and shape, and may have reached the posterior median ventral. But in C. 349 no contact face can be seen on the posterior margin of the anterior median ventral.

So although the main articulated specimen (C. 349) of the present study differs from *Coccosteus* in that the median ventrals do not meet, it may be that this is not always the case; certainly Heintz (20) figures (his text fig. 1.3) and gives a photograph (plate 2.2)

Fig. 22

AMV external surfaces

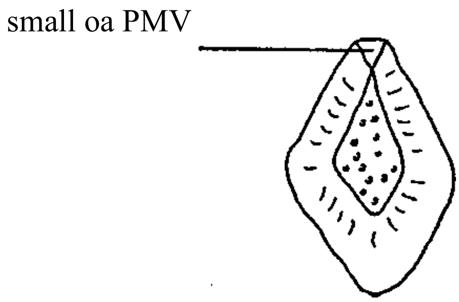
C. 362 C. 353



of a specimen that would seem to have the median ventrals in contact, and the length of the anterior median ventral in C. 362 is in accord with this view. It would, however, be unusual for such a great deal of fluctuation to occur in a species, involving not only the median ventrals remaining separated, but also the meeting of the anterior ventrolaterals between them.

Subsequently a search of the specimens of the BM(NH) has revealed an isolated posterior median ventral (BM(NH) spec. no. P52641) which is here drawn as a sketch (fig. 22g). There is clearly visible on the anterior margin of the external surface an overlap area of triangular shape (as in *C. cuspidatus*) for the reception of the anterior median ventral. It is probable that C. 349 is atypical in the light of this discovery, or has become disarticulated with the posterior projection of the anterior median ventral broken, although the latter is difficult to envisage. The smallness of the oa in P52641 still leaves room for doubt.

Fig. 22g PMV BM(NH) no. P52641 sketch



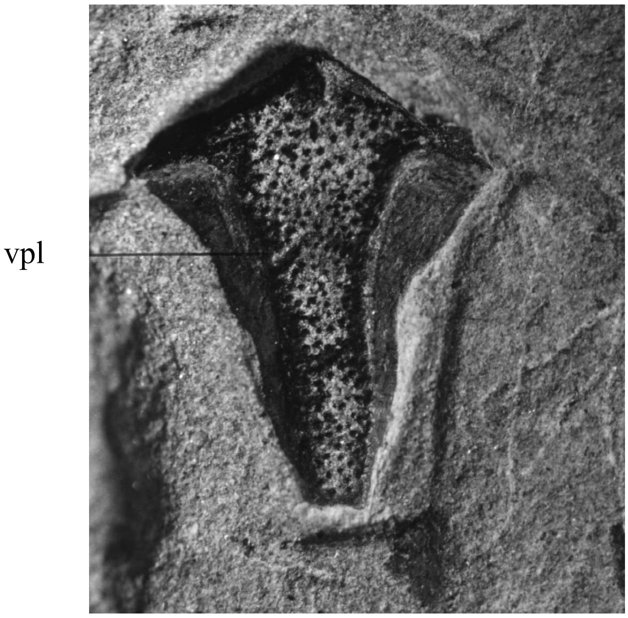
Heintz (20) did not record a ventral sensory canal on the anterior median ventral, and his text figure 1.3 shows no ventral canals. Miles has recently written (23), in regards of the canal on the anterior median ventral:

> "In *Coccosteus* the groove for this sensory line scribes a shallow arc on the surface of the bone (Fig.8A); in *Millerosteus* the line is not represented in the fossils (Fig.8D)." (page 432)

Yet this canal is clearly visible on C. 362 (vpl, fig. 22a) as a pronounced, if shallow groove. It is deeper on the left than the right side, although visible for its entire length. As in *C. cuspidatus* the canal in *Millerosteus* is arc-shaped. Plate 8.

Plate 8

AMV of C. 362



PVL of C. 340

The posterior median ventral (external surface fig. 22g; visceral surface fig. 5) is overlapped by the ventrolateral plates anterolaterally and by the posterior ventrolateral plates posterolaterally. It is assumed that it is overlapped anteriorly by the anterior median ventral as a rule, noting the exception previously mentioned.

The anterior ventrolateral plate (visceral surface figs 5, 22c; external surface figs 22d, e, f) is curved laterally such that it reaches its highest point on the external (spinal) margin. Along this margin it forms the sub spinal and subpectoral wall of the flank armour; the subspinal margin occupies a length of 40% of the plate, the subpectoral emargination (sb.pect.em) 35% (cf. *C. cuspidatus* 17% and 56% respectively).

In discussing the family Coccosteidae, Miles stated (23):

> "The shoulder girdle of *Millerosteus* however differs from that of these forms in the absence of grooves representing the ventral neuromast system." (p 440-441)

In this he followed Heintz (20, text fig. 1.3) and Miles' reconstruction of the ventral thoracic plates (fig. 8D) was again reproduced in Miles (1966) (24) and by Stensiö in the *Traité* (25). But just as with the anterior median ventral plate, the anterior ventrolaterals have a sensory canal on their external surfaces, to be observed in BM(NH) specimens no. P52643, P52645 and P52642 (figs 22d, e, f respectively). As in *C. cuspidatus* this sensory line traverses the plate laterally, arcing so that in the mid point of the plate it is at its most posterior point. Mesially this canal joins with that discovered on the anterior median ventral, although no specimens showing this have been observed.

Anteriorly there is a contact surface on the visceral surface of the AVL for the IL and this is barely continuous (being restricted by a ridge on the exposed visceral surface) with that for the AMV on the mesial margin. More posteriorly there is a contact face for the PMV on the mesial surface, and this is continuous with that for the PVL on the ventral margin. The contact face for the Sp (infraspinal lamina, la.sp.) is very well defined and deep, and the visceral surface is greatly undercut at the posterior margin of this contact face, forming a recess into which the mesial surface of the spinal is located.

The region of the visceral surface that is undercut is greatly thickened and drawn out into a tapering projection facing posterolaterally. This lateral lamina has a much greater development in *Millerosteus* than in *Coccosteus* and is here referred to as the postspinal lamina (la.p.sp). This projection forms the anterior-most margin of the infrascapulocoracoid lamina (la.infscc) which slopes gently away posteriorly.

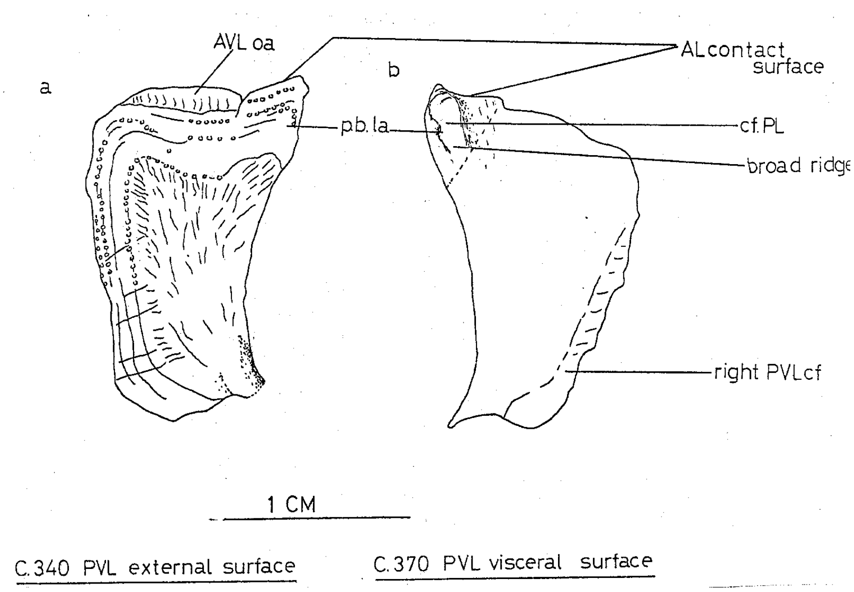
The anterior ridge that partially divides the contact faces of the interolateral and anterior median ventral continues posterolaterally and probably constitutes the mesial boundary of the area that in *C. cuspidatus* bore the anterior mesial angle of the coracoid process of the scapulocoracoid (dp.ama). In this region there is a very shallow depression in *Millerosteus*, but not a triangular one delineated as well as that in *C. cuspidatus*. More posteriorly there is a shallow depression which may correspond to what is referred to by Miles and Westoll (18) as the pericardial depression of the AVL (pc.dp.AVL), although the shallowness of this depression makes this somewhat conjectural.

The paired posterior ventrolateral plates (external surface fig. 23a; visceral surface fig. 5, 23b) are asymmetrical, the left overlapping the right strongly (ie in visceral view the left plate is overlapped by the right and a contact face is present on the former). The contact face becomes larger posteriorly occupying some of the ventral margin region.

Anteriorly there is a well defined overlap area for the anterior ventrolateral in *Millerosteus* that is clearly separated from the raised lateral postbranchial lamina (pb.la) [Plate 8]. These areas are not clearly delineated in *C. cuspidatu*s (Miles and Westoll (18) page 437 and 441) leading to a difference in interpretation regarding the composition of the posterior margin of the pectoral fenestra (discussed later under ‘restoration’). On the anterior margin of the postbranchial lamina there is a large area for contact with the anterior lateral (fig. 23a, b see its complement on AL fig. 21) absent in *C. cuspidatu*s.

Fig. 23

C. 340 PVL external surface C. 370 PVL visceral surface



The postbranchial lamina is therefore deeper in *Millerosteus* than in *Coccosteus*, and more abrupt in its disappearance ventrally. (It is shown incorrectly in Heintz (20) and Miles (23) – see fig. 24 for comparisons, see also fig. 23a, b. The anterior margin of the postbranchial lamina is not shown large enough in the previous restorations.) On the visceral surface of this postbranchial lamina there is a large contact face for the posterior lateral on which is situated a broad ridge. This triangular lamina is accommodated in the triangular recess formed by the posterior and anterior laterals (fig. 21a).

The external surface (fig. 23a) is characterised by three or four ridges parallel to the lateral, anterior and posterior plate margins; many of these ridges are composed of rows of tubercules. More mesially ridges and tubercules are absent, and this region is uniformly covered by pits and grooves, the latter being directed towards the ridges.

Only the interolateral of C. 349 (fig. 5 visceral surface) has been examined in the present study. This is similar to that for *C. cuspidatus*, having a ventral and ascending postbranchial lamina (the latter being developed to a lesser extent than in *Coccosteus*; in C. 349 it is seen in the horizontal plane due to flattening). Anteriorly there are overlap relations with the anterior median ventral and anterior ventrolateral (fig. 24), but unlike that of *Coccosteus* there is a long posterior lamina in *Millerosteus*, as noted by Miles (23; fig. 8D, reproduced as fig. 24,l.lat), which overlaps the anterior margin of the spinal plate. The dorsolateral corner of the ascending lamina overlaps the postbranchial lamina of the anterior lateral; this may be seen in C. 369 and in a cast of an unnumbered BM(NH) specimen. The anterior face of the ascending lamina is composed of a number of parallel ridges (C. 349, fig. 5); this face forms the posterior margin of the branchial region. The anterolateral margin of the anterior lateral is situated between the ventral and ascending laminae of the interolateral.

Restoration of ventral thoracic armour

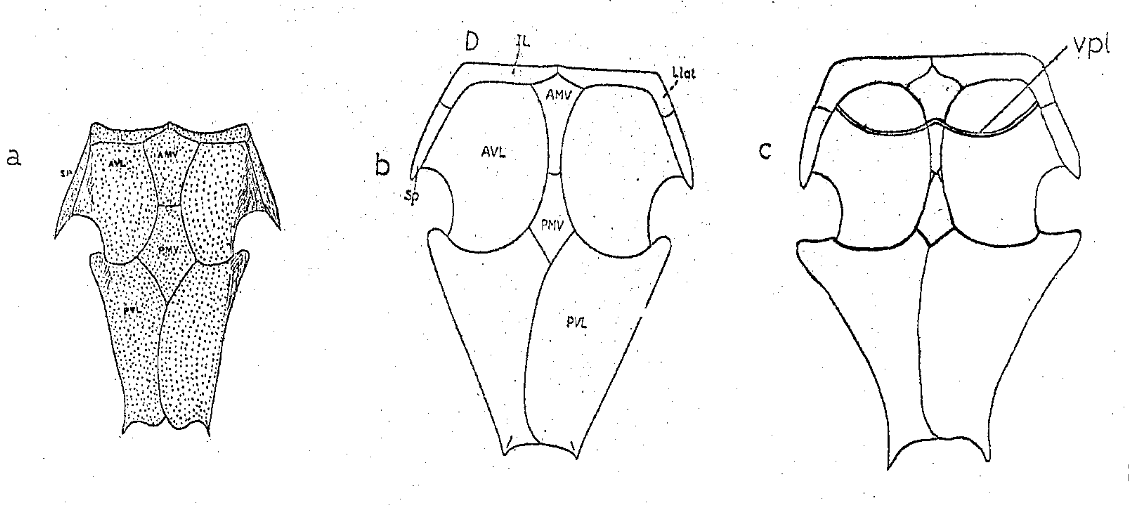
By the use of scale models of the dermal plates of the ventral thorax an attempt has been made to restore the armour to that seen in an articulated specimen flattened in the horizontal plane (fig. 24c). The restoration incorporates the new discoveries to arise out of the present study. The PVL plates differ markedly from those of Heintz (1938) and Miles (1964), although the latter was reproduced with modification from the former. The greatest difference is to be found in the shape and extent of the post-branchial lamina and in particular in the margin of this in contact with the AL (fig. 23a, b). The lateral projections on the posterior margins of the PVL plates are longer than those of Miles and similar to those shown by Heintz.

The AMV has a long and narrow posterior lamina (plate 8), unlike that in Heintz' restoration. There is still some doubt about the nature of the contact between the AMV and PMV. Apparently there is none in C. 349 and the AVL is in contact with its antimere. Yet in the isolated PMV plate P52641 (fig. 22g), although the exposed surface tapers anteriorly to a point, there is a small AMV overlap area, and the AMV plate C. 362 (fig. 22a) has a squared off, if narrow, area of contact for the PMV. The free surface of the PMV was obviously small (deduced from fig. 5, the isolated PMV, fig. 22a, and by the small area bordering it on the PVL, fig. 23a) and it is from this evidence that the present reconstruction is made (fig. 24c). This is unlike previous restorations of *Millerosteus* but similar to that of *Eldenosteus arizonensis* (Miles (1964) text-fig. 5), a coccosteid which Miles has compared to *Millerosteus* on other grounds (see 'affinities'). The examination of new specimens will throw more light on the nature of the contact of the median ventral plates, although it seems highly probable that it is different from that of *Coccosteus* and previous restorations of *Millerosteus*.

The previously undetected ventral neuromast system (vpl) is shown on the restored ventral thoracic armour. It is seen to resemble the position occupied by its counterpart in *C. cuspidatus*.

Fig. 24

Cf. PMV, PVL and vpl



Ventral thoracic armour a. Heintz (1938). b. Miles(1964). c. new restoration

Restored thoracic armour

An attempt has been made to restore the thoracic armour as it would have appeared in life using plates constructed to the same scale and by the building of three dimensional models (fig. 26).

The AVL is transversely arched, as is the PVL, and together with the IL and Sp these plates are connected to the flank armour. As already stressed the anterior lateral margin of the PVL has a complementary contour to its counterpart on the AL. The postbranchial lamina of the PVL overlaps the PL (fig. 21a) and fits into the triangular recess formed at the free boundaries of the AL and PL (unlike that shown in the restoration of Miles (23), fig. 21b). Unlike *C. cuspidatus* there is a clear demarcation between the postbranchial lamina that fits this recess and the overlap area for the AVL (fig. 23a, b).

Miles and Westoll asserted that (18):

> "The anterolateral region of the outer surface of the PVL is devoid of ornament and cannot always be distinguished from the more mesial area overlapped by the AVL." (page 441)

So although they showed the AVL oa to extend some large distance into the postbranchial lamina on their text-fig. 41a, on their restoration (text-fig. 43) they show the posterior margin of the pectoral fenestra as formed by the postbranchial lamina of the PVL. Yet if the AVL has contact with the AVL oa it would almost completely exclude the PVL from forming a boundary of the pectoral fenestra.

In *Millerosteus* the position is far clearer. The entire anterior margin of the postbranchial lamina is adjacent to the posterior margin of the AL; immediately mesial to this lamina the AVL overlaps (fig. 22a, b). Here, then, it is even more probable that the PVL could NOT have formed a large part of the boundary of the pectoral fenestra and from the evidence one

can only conclude that its role in the formation of the boundary of the pectoral fenestra was, in fact, negligible. It seems likely that the dorsal and ventral boundaries of the fenestra were formed by the AL and AVL and that these converged near the posterior border, as is shown in fig. 26. In the light of the new evidence uncovered for *Millerosteus* it may be necessary to revise the restoration of the pectoral fenestra in *Coccosteus*.

Anterolaterally the AL is drawn out into a projection, and the Sp stops short of this (cf Miles, fig. 21b; Heintz, fig. 24a; Stensiö, fig. 25), while the anterior margin of the Sp is not tapering but quite sharply angled.

The posterior spine is shown in its correct length and is not restored turning dorsally (cf Stensiö, fig. 25), as Heintz has suggested it should be, as no evidence from the many MD plates examined corroborates this view in any way.

The main branch of the lateral line canal (lc) is drawn, as is the dorsal branch (ld). Note the obtuse angle formed by the latter at its emergence (it is not shown in Miles (23) text-fig. 8G); this was found to be the case in all specimens examined, although it is a rare occurrence in *C. cuspidatus* and never quite turns as sharply when the angle is obtuse.

The MD, ADL(Pt), PDL(Sclm) and PL(Aclm) plates are shown with incorrect shapes in Stensiö's restoration (fig. 25). Miles (23, his text-fig. 8B, C) has corrected these and shows a correct PL/PDL junction (ie as it occurs in other coccosteids) but he has incorrectly drawn the PVL oa.

Restoration of head shield

In certain specimens the head shield, or particular regions of it, are preserved in an uncrushed and unflattened state, and it is from these, together with the use of models with scaled-up plates, that the shape of the head shield and the relationship of the plates have been deduced (fig. 26).

The nuchal is preserved uncrushed in an unnumbered BM(NH) specimen and it shows the plate to be traversely bowed, high domed and with a flattened area on the crown. The roof of the head shield, as in *C. cuspidatus*, was fairly broad and composed mainly of a flattened area of triangular shape, with the apex at the crown of the nuchal and the base between the orbits. Prominent ridges are present over the orbits on the PrO plates, slightly bowed supraorbitally but descending steeply on the anterior preorbital lamina (seen in C. 369, best observed over the right orbit where the original profile has presumably been retained). The dermal head shield is altogether deeper posteriorly than Stensiö has shown in his restoration (fig. 25), and broader transversely, as is the case for *Coccosteus*. Anterior to the nuchal the profile of the skull roof is almost flat, with the exception of the pronounced supraorbital ridges.

One of the main grounds for divergence in the present restoration arises from the discovery of the very deep anterior lamina of the rostrum and the enormous tubercules with which it is covered to its extremity. As already discussed, on account of this the snout could not possibly be cartilaginous as Stensiö has shown (although labial palps were probably present on the subnasal region). Furthermore the discovery of the interfenestral process on the PN indicates conclusively that an anterior (incurrent) nostril was present on the armoured snout (as in *Coccosteus*). The rostral plate protrudes some distance in front of the other bones of the snout and is unique in a number of respects. In *C. cuspidatus* Miles and Westoll have shown there to be a gentle contour in the rostral plate such that it arcs through 90˚. This is quite different from

the condition encountered in *Millerosteus* where the anterior descending lamina of the rostral makes an abrupt angle of almost 90˚ with the posterior lamina. This angular snout of *Millerosteus* is further made more grotesque by the covering of the whole area in large (presumably protective) tubercules.

The cheek region has been restored according to the discoveries brought to light in the present study (lack of PtO/PSO contact, contact of PNu/PM excluding marginal from the posterior boundary of the head, shorter suborbital lamina of PtO; cf. Stensiö's restoration). Also the shapes of the M, PM, SM or I, PSO, PtO, SO and PNu differ from those of the previous reconstruction, in some cases greatly (eg PtO, SO, M), but in the others only on points of detail.

The sensory canals of the head shield are drawn, and seen to differ in detail only from Stensiö's (eg his supraorbital canal crosses the central plate too mesially, it should cross the lateral boundary of the anterior lamina). The newly discovered canal on the PSO is included.

Although the SG has not been described for lack of specimens the IG is shown restored, the restoration being based on the examination of three partial specimens. It is seen to be very narrow, but with very large, tapering conical teeth positioned, as in other coccosteids, some distance behind the anterior margin of the IG.

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Fig. 25

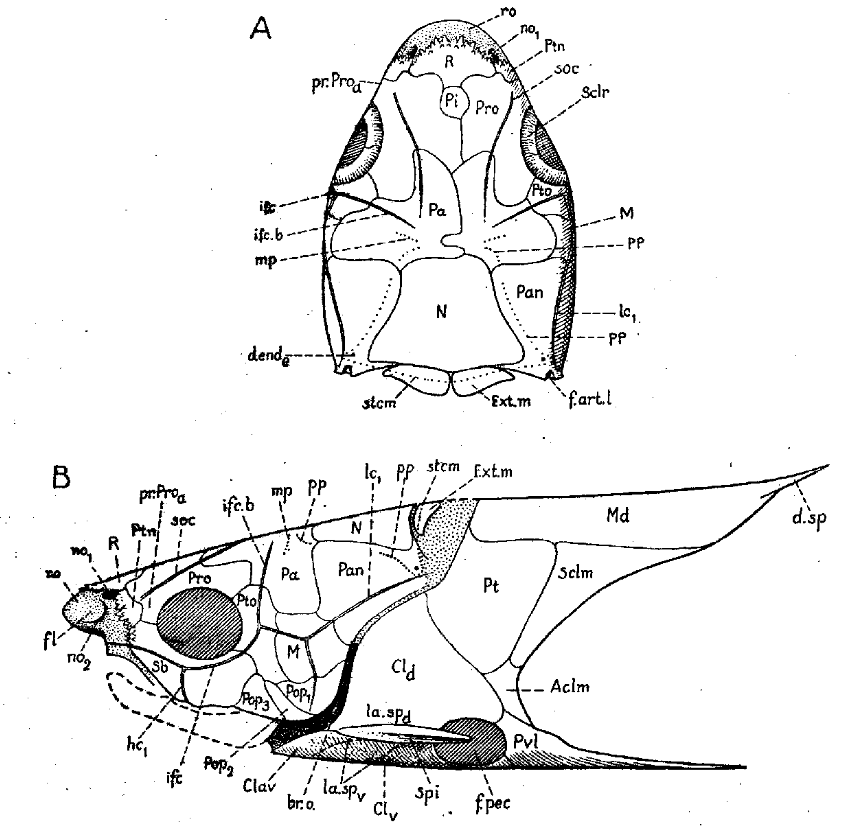
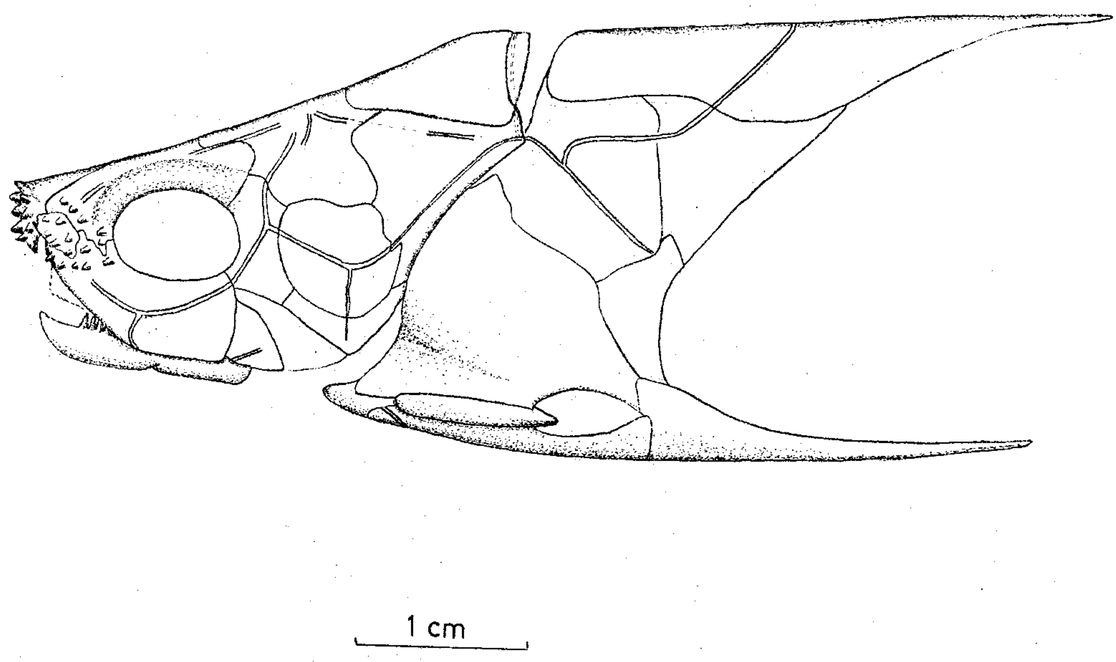


Fig. 74. ***Millerosteus minor*** **(MILLER; – "*Coccosteus*" *minor*). *A*, attempted restoration of head in dorsal view. *B*, attempted restoration of head and shoulder girdle in lateral view. The two restorations made on the basis of the sketches and plates published by HEINTZ in 1938 (1938a). Approximately × 2.5. Soft parts of snout shaded with delicate stippling. In fig. *B*, the soft tissue between the exoskeletal skull roof and the exoskeletal shoulder girdle also shaded in this way.**

Aclm, **anocleithrum ("posterior lateral" plate); *Clav*, clavicle ("internal" plate); Cl_d, dorsal cleithral ("anterior lateral" plate); Cl_v, ventral cleithral ("anterior ventro-lateral" plate); *Ext.m*, medial extrascapular plate; *M*, marginal plate; *Md*, median dorsal plate; *N*, nuchal plate; *Pa*, parietal; *Pan*, paranuchal plate; *Pi*, pineal plate; Pop_1, Pop_2, Pop_3, dorsal, middle and ventral preopercular plates, respectively ("postmarginal", "internal" and "postsuborbital" plates, respectively); *Pro*, preorbital plate; *Pt*, posttemporal ("anterior dorso-lateral" plate); *Ptn*, postnasal plate; *Pto*, postorbital plate; *Pvl*, posterior ventro-lateral plate; *R*, rostral plate; *Sb*, suborbital plate; *Sclm*, supracleithral ("posterior dorso-lateral" plate); *Sclr*, sclerotic ring; *Spi*, spinal plate; *br.o*, branchial opening (external aperture of gill chamber); $d.end_e$, external aperture of exoskeletal division of canal for endolymphatic duct; *d.sp*, probable dorsal spine fused with *Md*; *f.art.l*, lateral articular fossa formed by paranuchal plate; *fl*, probable valve of skin hanging down in front**
of excurrent nostril; *f.pec*, pectoral fenestra (filled by fin-bearing part of scapulo-coracoid; see STENSIÖ 1959); hc_1, foremost part of supramaxillary sensory line (foremost part of "horizontal pit line of cheek"); *ifc*, infraorbital sensory line; *ifc.b*, central sensory line; $la.sp_d$, supra-spinal process of dorsal cleithral; $la.sp_v$, infra-spinal process of ventral cleithral; lc_1, cephalic division of main lateral line; *mp*, middle pit line; no_1, no_2, incurrent and excurrent nostrils, respectively; *poc*, preopercular sensory line; *pp*, posterior pit line; $pr.Pro_a$, exoskeletal antorbital process; *ro*, rostral part of snout without dermal bones; *soc*, supraorbital sensory line; *stcm*, supratemporal sensory line commissure.

Fig. 26

[Restoration of *Millerosteus minor*]



Conclusions: Systematic position and Affinities of *Millerosteus*

Stensiö erected the genus *Millerosteus* in 1959 (22; page 6) and it has remained since then monotypic, containing only '*Coccosteus minor*' (now *Millerosteus minor*). In 1963 (19; pages 392, 399-400) he gave a diagnosis of *Millerosteus*, based on one specimen belonging to D. M. S. Watson and guided by the earlier description of Heintz (20). Most of his analysis was concerned with the orbital region; in fact, of the ten points listed to distinguish *Millerosteus* from *Coccosteus* seven were a result of this limited area of study, and one with which this thesis has not concerned itself. Point eight is

"the absence of an interfenestral process on the postnasal plate" page 400

while nine and ten are concerned with the fusion of the cheek to the skull roof and resulting jaw suspension modifications.

It has been conclusively shown from the present study that the interfenestral process is present on the postnasal plate (see plate 6) and thus point eight is invalidated. The remaining two points are, as will be seen, functional modifications and not of great phylogenetic significance.

Furthermore Stensiö (1963) created a new family, the Millerosteidae, one of whose characteristics was, as a result of their being only one member, the lack of an interfenestral process on the postnasal plate. Miles and Westoll (1963) (10), however, included *Millerosteus* in the Coccosteidae (page 185) but without explanation of reasons, for *Millerosteus* was not discussed.

Miles, though, in 1964 (23) indicated his acceptance of the new family, but made the following assertion:

"The Millerosteidae, on the evidence of the thoracic neuromast system [ie. the lack of it], are a specialised off-shoot of the Coccosteidae" page 444.

This has also been shown to be incorrect, for the sensory canal has been detected during the present study on both AVL and AMV (plate 8, vpl on AMV) in a position occupied by its counterpart in *C. cuspidatus*.

Not only is the ventral neuromast system now known to exist, but the small postsuborbital canal, which is probably an extension of the supraoral (supramaxiliary) sensory canal, has now been shown to be present (plate 7), as it is in *Coccosteus, Plourdosteus*, *Dickosteus* and *Clarkeosteus*.

The anterior descending lamina of the rostral plate is apparently a fluctuating feature among coccosteids; it is interesting that it is a notable feature on the snouts of all the Scottish forms (*Coccosteus*, *Dickosteus*, *Watsonosteus* and now *Millerosteus*) although seemingly absent in *Plourdosteus*, *Clarkeosteus* and *Protitanichthys* (Miles, 1966).

The removal of other anomalies of Stensiö's restoration, such an the marginal forming part of the posterior margin of the head shield and the postorbital contact of the postsuborbital, adduces yet more evidence in favour of the author's contention that *Millerosteus* should be retained within the Family Coccosteidae. In fact, if Miles' definition (24, pages 28-30) of the Family Coccosteidae is to be accepted, *Millerosteus* must now be considered a near typical member in all respects except those relating to the check region (ie. the SO does not bear a large postorbital lamina, a large PM is present and the cheek is fused to the skull roof, whereas there is only a loose connection in other coccosteids, Heintz ((20) page 4). Yet, taken in conjunction with other evidence, such as the highly ossified neural arches* (from which one may assume a powerful muscular tail), a small extent of jaw shortening caused by the anterior shift of the PSO (itself a function of the lack of the postorbital lamina of the SO), which is indicative of a snapping jaw action, and the large stabbing 'teeth', it is readily seen that a functional complex is involved. *Millerosteus* was

* mistaken by Watson (1935) for 'well ossified vertebral centra' (page 159).

undoubtedly, from the evidence of the ‘teeth’, highly predaceous and probably hunted by darting at its prey and stabbing with its teeth. Perhaps the peculiarly heavily ossified and tuberculated rostrum was developed in order to afford protection of the snout on these occasions.

To conclude, *Millerosteus* was a coccosteid whose adaptation to a predatory snapping mode of life necessitated changes in the cheek in response to altered jaw kinetics. But this is superimposed on the basic coccosteid pattern and it is only in the shape of certain cheek plates that *Millerosteus* now differs significantly from other members of that Family; all supposed specialisations have been shown not to exist in *Millerosteus*.

Amended Diagnosis – *Millerosteus minor* is a very small coccosteid, with head and trunk armour rarely attaining a length of more than 70 mm, of which ca. 45% is occupied by head shield and ca. 50% by the trunk shield. The length of the head shield is ca. 85% of its maximum breadth in flattened state; the cheek is fused to the skull roof. Nuchal plate covers ca. 33% of length of head shield, pp, mp, csc and soc remain separate on C. PrO has extensive overlap relations with its antimere, supraorbital ridge on anterior descending and supraorbital laminae of PrO; soc terminates on PrO. PNu meets PM. M large and round. PtO elongated dorsoventrally but has only small area of contact with SO, PtO meets PM. R with well developed dorsal lamina and very heavily ossified anterior descending lamina covered to its ventral extremity with large tubercules. PN similarly heavily ornamented, interfenestral process present. I or SM wider posteriorly, separates PSO and PtO. PSO triangular and with sensory canal. Suborbital lamina of SO deep and heavily tuberculated anteriorly, negligible postorbital lamina. Inferognathal narrow with possibly 8 high conical teeth in dentigerous region, anterior region devoid of teeth, long posterior non-biting division. MD long (width ca. 45% length) with long posterior spine accounting for ca. 25% of length; very low keel and carinal prowess, although well developed. ld on ADL diverges at obtuse angle, PDL has posterior projection lateral to MD. AL with long supraspinal lamina (ca. 55% length)

and short suprapectoral lamina (ca. 33% length). Long Sp although it does not reach the anterior boundary of AL. Postbranchial lamina of PVL large and accommodated in triangular recess formed by AL and PL, long PVL margin in contact with AL; posterolateral projections on PVL. AVL with long infraspinal lamina (ca. 55% length); ventral sensory canal on AVL and AMV. AMV and PMV narrow and former elongated. Posterior lateral process on IL. Well developed pelvic girdle and neural and haemal spines; very heavily ossified neural arches.

Where must we look for the affinities of *Millerosteus*? Miles (1964) noted that *Eldenosteus* shared with *Millerosteus* a long infraspinal lamina on the AVL. The length to the posterior of the spinal lamina is 60% of the total length in *Eldenosteus* and 55% in *Millerosteus*. Miles listed a number of features in which the two genera differed. One of these was the relative shapes of the median ventral plates, these being shown as broad in Heintz' account of *Millerosteus* but they are very narrow in *Eldenosteus*. It has been shown in this thesis that Heintz was incorrect and that they are also very narrow in *Millerosteus*. In fact the PMV depicted by Miles for *Eldenosteus* (his text-fig. 3B, page 436) is almost identical in shape to *Millerosteus* PMV no. P52641 (fig. 22g) in respect of the small AMV oa and the tapering of the free surface anteriorly. However, similarities between the two genera are in all probability due to the retention of primitive characters (eg long spinal lamina), as Miles himself pointed out, and may not be indicative of a close phylogenetic relationship.

With Gross's discovery (17) of *C. cf minor* in the Baltic it would seem that this area may have been an extension of Lake Orcadie or perhaps a separate Middle Devonian lake in which were to be found the relatives of *Millerosteus*. Indeed a search of the literature reveals a *C. acuminatus* (known from one MD from the Rhineland) reported in Gross (1937). This has a long posterior spine and is of *Millerosteus* size. Later (1940) Gross reports *C. orvikui* from the Baltic, again with a small MD with a long spine. It is possible that these are synonyms for *Millerosteus* (which may thus not be a monotypic genus) and that the affinities of *Millerosteus* are to be sought in the Baltic.

ABBREVIATIONS USED IN TEXT-FIGURES

ADL	anterior dorsolateral plate
AL	anterior lateral plate
ant.des.proc	anterior descending process
AVL	anterior ventrolateral plate
C	central plate
cf.	contact face
ch.rdg.	channel for ridge on nuchal overlap area
cr.pr	carinal process of MD
csc	central sensory canal
d.end	ductus endolymphaticus
dp.ama	depression for anterior mesial angle of scapulocoracoid
dp.mc	depression in posteromedian cusp of nuchal
dp.sv.sw	depression in nuchal for supravagal swelling on PNu
Esc	extrascapular plate
fen	fenestra
gl.pr	glenoid process
gr.ssc	groove receiving semicircular canal ridges
h.sp	haemal spine
IL	interolateral plate
I	internal plate
ifc	infraorbital canal
if.pr	interfenestral process of PN
IG	inferognathal
ioc	infraorbital canal
ioc.ot	otic branch of infraorbital canal
k	keel
la.asp	posterior ascending lamina [of nuchal]
la.infscc	infra-scapulocoracoid lamina of AVL
la.p.sp	postspinal lamina [of AVL]
la.spv	infraspinal lamina of AVL
lc	main lateral line canal
ld	dorsal branch of main lateral line canal
l.lat	posterior lateral lamina of IL
M	marginal plate
mc.Nu	postero-median cusp of nuchal
MD	median dorsal plate
mp	middle pit line
n.arch	neural arch
n.sp.	neural spine
Nu	nuchal plate
oa	overlap area
occ	occipital cross commisural sensory canal
P	pineal plate
pb.la	postbranchial lamina [of PVL]
pc.dp	pericardial depression [of AVL]
PDL	posterior dorsolateral plate
pdl	posterior dorsal lamina of M
Pelv	pelvic girdle
P.fen	pectoral fenestra
pin.pit	pineal pit
PL	posterior lateral plate
PM	postmarginal plate
pmc	postmarginal sensory canal
PN	postnasal plate
Pnu	paranuchal plate
p.pts.	Nu paired pits in the visceral surface of nuchal

PP	posterior pit line
PrO	preorbital plate
PSO	postsuborbital plate
psoc	postsuborbital sensory canal
PtO	postorbital plate
PVL	posterior ventrolateral plate
R	rostral plate
sc.cor	scapulocoracoid
sb.pect.em	subpectoral emargination [of AVL]
SM	sub-marginal plate
SO	suborbital plate
soc	supraorbital sensory canal
sorc	supraoral sensory canal
Sp	spinal plate
subgl.pr.	subglenoid process
ven.rec	ventral recess of R
vpl	ventral neuromast line
zyg	zygopophysis

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